MICROSTRATIFICATION OF PHYTOPLANKTON IN SELECTED MINNESOTA LAKES

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Alan Lee Baker

2

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ABSTRACT

A study of the entire phytoplankton community in three mesotrophic lakes in Minnesota revealed the presence of thin strata of individual populations along the depth axis. The presence of the strata was confirmed with continuous profiles of optical density. Sharp gradients of several physical and chemical parameters were observed in the vicinity of the algal strata. Activity of the strata was measured by productivity and plankton-trap analysis. The apparent magnitude of seasonal succession was related to several expressions of dominance. Ordination of species along the depth axis was invariant in the study lakes. The possibility of the mutual exclusion of seasonal succession of species and physical stability of the lake system was discussed.

Experiments with laboratory columns containing metalimnetic water demonstrated the primary influence of light on vertical migration of the phytoplankton, and of temperature gradient on the formation and persistence of algal strata. Depth ordination developed in the columns similar to that in the study lakes.

Finally, I wish to compliment my parents for their long patience during the study which they in very many ways influenced some time ago.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

INTRODUCTION

Although the spatial distribution of phytoplankton in lakes has been investigated in some detail by several investigators, many questions still remain unanswered. These especially concern vertical distribution patterns of individual species, and of the entire phytoplankton community, an aspect which has intimate bearing on seasonal succession and the origins and fates of individual algal populations. Previous studies provide ample evidence that individual species tend to form strata during summer thermal stratification (Ruttner, 1930; Grim, 1939; Eberly, 1959; Lund et al., 1963; Findenegg, 1964; Moss, 1969), but none have dealt with the phenomenon with sufficient precision to allow the adequate study of any gradients or strata of phytoplankton which may be less than 1 m in vertical extent.

Stratification of phytoplankton has been observed even in the least stable of lakes, including the large polymictic tropical lakes in which diurnal mixing occurs (Baxter et al., 1965). Thus differences in vertical distribution patterns of phytoplankters may be present in lakes except during periods when complete mixing of the entire depth column is occurring.

The development of algal strata is greatest in lakes having the least vertical mixing, such lakes being characteristically wind-protected, small, and relatively deep (Baker and Brook, 1971). Lakes of this type are particularly abundant on glacial moraines in central Minnesota, Wisconsin, Manitoba, and Ontario.

The accuracy of both the measurement and modeling of lake metabolism, including phytoplankton productivity (Patten, 1968;

Fee, 1969), depends directly upon how adequately phytoplankton distribution is represented when collecting samples or constructing models. For example, samples are frequently taken only from the surface of a lake and are assumed to be representative of the entire lake. Models often depend on the same simplistic assumption. Clearly measurement or models are of value only when the algal distribution is homogeneous. In consequence, this study has been undertaken at least in part to investigate the extent to which heterogeneity in vertical distribution of the phytoplankton occurs. An additional objective has been to determine whether individual species concentrate as strata and so are restricted to a relatively narrow depth range; also whether species stratify independently or in groups.

Certain phytoplankton species are considered to be stenothermal, others eurythermal. Temperature is thus implicated as an important factor in determining their distribution, perhaps the most important (Ruttner, 1953 and Weisenburg-Lund, 1909). The present study includes observations of temperature gradients within short depth-intervals (10 cm), suggesting the presence of a microstructure similar to that in Loch Ness (Simpson and Woods, 1970). An optical density microstructure similar to that found much earlier in several Wisconsin lakes (Whitney, 1937, 1938) also became apparent from the close-interval sampling procedures followed (Baker and Brook, 1971). The presence of such a microstructure in the vertical profile of lakes, as well as a microstructure of several dissolved ions, supports the hypothesis that a lake is not a simple one-compartment

system which can be understood by studying any single part, but rather is a series of relatively independent layers, each differing from those above and below in temperature, light and nutrients. Each layer may have either clear or diffuse boundaries, and even may be within itself heterogeneous. The strata may be unmeasurably thin, with the result that profile gradients of physical and chemical parameters appear to be continuous. An attempt to relate phytoplankton distribution to environmental parameters and their gradients was made by sampling at closely-spaced depth intervals and comparing the microstructure of the various profiles (Baker, 1970).

Although the primary objective of critically examining and describing the vertical distribution of phytoplankton strata, several additional questions arose. For example, are the stratified populations physiologically active, or are the strata simply vestigial remains, i.e. inactive, waning populations which have sedimented into a layer of water having a specific gravity similar to that of themselves? In attempting to provide answers, studies were carried out on sedimentation of species within the lake, of in situ productivity, and of stratification in experimental laboratory columns.

A comparison was made of several diversity indexes, along with depth profiles of phytoplankton diversity. The profiles carry implications relative to speculations advanced by Margalef (1958, 1963, 1968).

DESCRIPTION OF THE STUDY LAKES

Three lakes were selected for study on the basis of information gathered previously by limnology classes under the direction of Dr. James Underhill at the University of Minnesota's Lake Itasca Forestry and Biological Station. Of particular interest in this regard were profiles of dissolved oxygen found to be strongly positive-heterograde. The profiles suggested the presence of metalimnetic, rather than epilimnetic, peaks in productivity. The lakes, Deming, Arco, and Josephine, are located in Itasca State Park, Clearwater County, Minnesota, T143N, R35-36W, elevation 443 m, near Lake Itasca, headwater of the Mississippi River (Fig. 1). The lake basins are small with a large "relative depth" (Figs. 2, 3), and are protected by the surrounding forested watersheds from even severe winds. (No morphometric data of Josephine Lake were available.)

The terrain surrounding the study lakes was formed during the late Wisconsin glaciation when the St. Louis sublobe stagnated in the region forming what is known as the Itasca Moraine (Wright, 1968). Many basins scattered over the moraine are considered to be ice-block depressions. The oldest lacustrine sediments have been dated at 11,000-12,000 years B.P. (McAndrews, 1967).

A mature mixed deciduous and evergreen forest covers the watersheds of the three study lakes, the dominant trees being Pinus resinosa, Populus grandidentata, Betula papyrifera, and Pinus strobus. Alnus rugosa lines the shores. Within each of the three basins only a few emergent plants occur, of which the most obvious is Brasenia schreberi. Other rooted aquatic plants

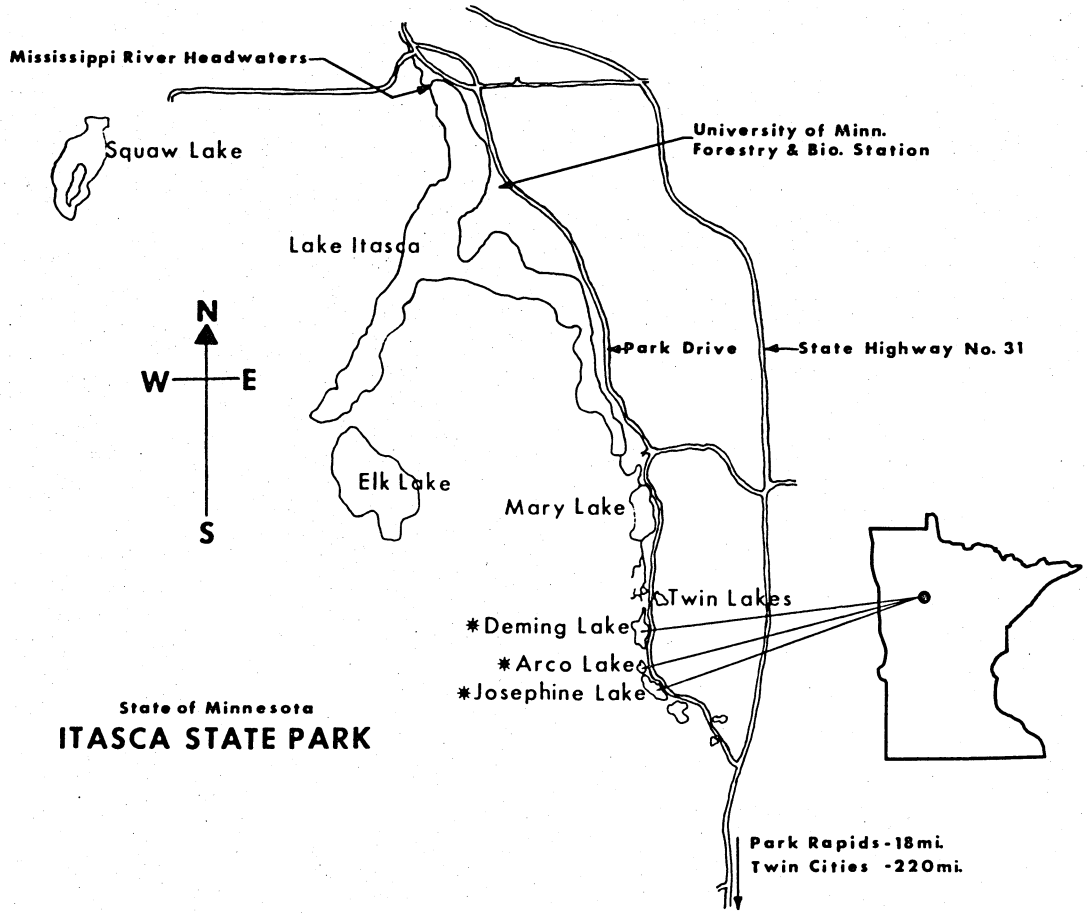


FIG. I. LOCATION OF THE STUDY LAKES WITHIN ITASCA STATE PARK, NORTH-CENTRAL MINNESOTA. (* STUDY LAKES)

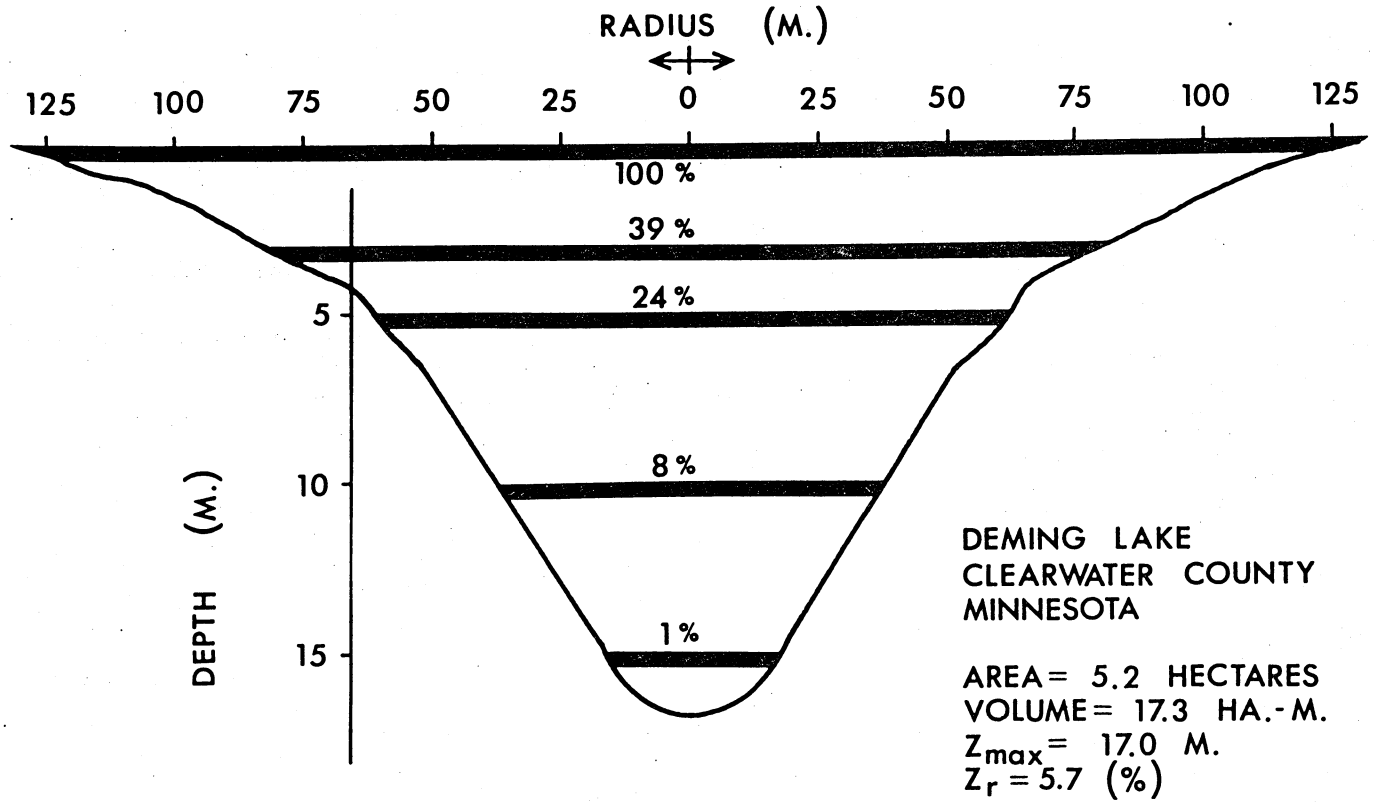


FIG. 2. SCHEMATIC CROSS-SECTION OF DEMING LAKE (AFTER HYPSOGRAPH). PERCENTAGES WITHIN THE FIGURE REFER TO THE AREA OF THE LAKE SECTION AT THAT DEPTH, RELATIVE TO THE SURFACE AREA.

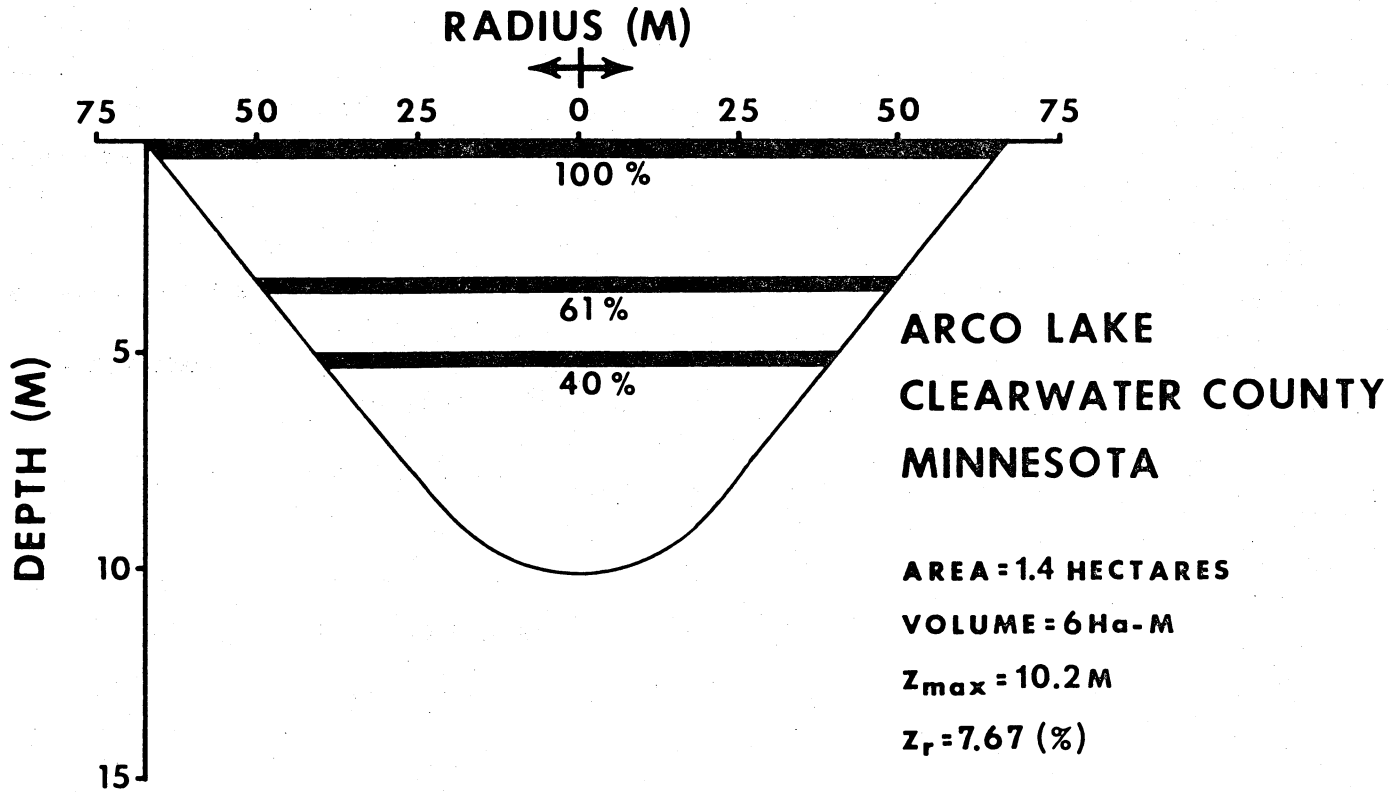


FIG. 3. SCHEMATIC CROSS-SECTION OF ARCO LAKE. (CF. FIG. 2.)

were surveyed by Hooper (1948) and Bland (1970). The littoral zone is limited in extent by the steepness of the basins and high extinction of sunlight within the lakes.

The basins have no permanent inlets or outlets, although an intermittent stream draining a marsh into the south end of Deming delivers a small volume of water during snow-melt and after large storms. The water-sheds are small, and surface runoff during heavy rainfall is usually limited to the grassy slopes along the roadside of Deming and Josephine. As there are no surface springs entering the lakes, the majority of water input must be as direct rainfall and as sub-surface seepage. Although no direct measurements were made, water-level fluctuation appeared to be less than 50 cm between 1967 and 1971. Hooper (1948) reported fluctuations greater than 1 m occurring during the early 1940's.

Although many lakes in the vicinity are hard-water with more than 150 ppm $CaCO_3$ as a result of weathering of the calcareous till of the Itasca moraine and inflow via streams and springs from large watersheds, the three study lakes have a hardness of less than 25 ppm $CaCO_3$. The surface waters have a conductivity of 60 to 80 micromhos/cm. Total dissolved phosphorus was undetectable in the epilimnion during the summer. Dissolved iron and magnesium decreased during the summer to 20 ppb and 190 ppb respectively from 110 ppb and 2430 ppb. Positive gradients of these and other dissolved substances occurred within the thermocline and downward through the hypolimnion. Near the bottom (17 m) of Deming Lake, phosphorus exceeded 63 ppb, iron

7200 ppb, and magnesium 3700 ppb. These profiles suggest the presence of meromixis in Deming Lake (cf. Kjensmo, 1968).

During the winter, the dissolved ion gradients persisted in all three lakes, although complete mixing in Josephine temporarily lowered ion concentrations in the bottom (10 m) waters. Under the ice the surface concentrations of iron, phosphorus, and magnesium increased. The concentration of NH_4-N was 665 ppb at the surface, and 7,000 ppb at 16 m in Deming Lake. The temperature profiles of the lakes probably were influenced more by direct solar and sky radiation than by wind activity, because of the wind-protected location. The regional climate is continental, with temperature extremes of from greater than 33°C in summer to less than -40C in winter. A plot of the medians of the daily temperatures recorded at the Itasca Biological Station (I.B.S.) Weather Station during the period 1960-1968 resembles in shape a cycloid, with a maximum in late July and a minimum in late January (Appendix III). Daily temperature variation is relatively large during the winter and small during the summer. Surface lake temperatures tend to reflect atmospheric temperatures, rising to a maximum in late July or early August. The lakes are usually ice-free by late April, although the date of ice-melt varies from early April to mid-May (Appendix IV).

METHODS

Frequent profiles of light, temperature, and optical density were taken in lakes Josephine, Arco, and Deming, especially during ice-free periods. Similar profiles were also obtained,

though less frequently, from several other lakes within Itasca State Park.

A. Light intensity was determined with a Whitney-type submersible photo-cell. The relative intensity units taken at various depths are expressed as a percentage of the surface intensity value, I_0. Most measurements were made within two hours of solar noon, at intervals of 0.5 m.

B. Lake temperature was estimated with a submersible thermistor-thermometer (Precision Scientific Co.) calibrated in the temperature range 0.00 - 30.00°C with a standard calibrating thermometer. Temperature was estimated to the nearest 0.1°C, and was assumed to be within a range of $\pm$0.1°C, of the real value. The probe reached equilibrium with the surrounding water in less than 30 seconds, no further change in needle deflection being detectable after longer exposure. The depth interval between measurements was varied, and depended upon the temperature gradient between depths. Within the steepest gradients, intervals of 10 cm were chosen. Closer measurement was difficult from the relatively unsteady platform of the boat.

C. Optical density of lake water was estimated with a submersible transmissometer (Kahl Scientific Co.) having a variable-length light path and a 12v incandescent lamp. The instrument had only one sensitivity range. Full-scale deflection of the microammeter was achieved by adjusting the light-path length. Once the appropriate length (35 cm) had been found, it was used consistently in studies of Deming, Josephine, Arco, and several other lakes with similar ranges of O.D. In several larger

lakes, the maximum O.D. value encountered was much lower than that found in the smaller lakes, in which case it was necessary to use a light path of 1 m. The lamp intensity in every case was calibrated in air with a 0.60 neutral density filter, by setting the meter reading arbitrarily to 0.40 O.D. (A log scale was drawn on the meter in place of the % Transmission scale.) Absorption of light due to water color was not measured, and therefore was not subtracted from the O.D. readings. The influence of color on the O.D. value must have been greatest near the mud-water interface, where the water was visibly yellow.

After the surface-water O.D. value was recorded, the probe (which consists of a horizontal light beam and a photocell) was lowered slowly until a change was apparent on the meter, and the value was recorded to the nearest 0.001 O.D. unit. The procedure was repeated to the bottom of the lake. It was impractical to take readings at depth intervals of less than 5 cm.

D. Water samples. A Van Dorn water bottle was used for all water collections during 1967-1968, and as a result samples were taken at depth intervals of 0.5 m. Furthermore, these samples were integrated over the length of the bottle, nearly 0.5 m. Samples taken in 1969-1970 were collected with a microsampler (Baker, 1970). The samples were collected at 0.2 m depth intervals in regions where a microstructure in O.D. was found, otherwise at 0.5 or 1.0 m intervals. Integration of these individual samples was limited to a depth interval of no more than 3-4 cm.

E. Dissolved oxygen was determined either by the Winkler technique (azide modification), or with a portable meter having

a submersible silver-lead galvanic cell (Precision Scientific). The meter was calibrated daily with a Winkler determination of a surface sample.

F. Phytoplankton counting was carried out with the inverted-microscope technique (Utermohl, 1931) and a Unitron microscope. A measured volume of lake water containing a 1:60 concentration of modified Lugol's preservative (15 g I_2, 15 g KI/L) was allowed to settle for 24-48 hours in a 5 or 10 cc counting chamber (Zeiss). The plankters were identified and counted, and the counts of individual species were converted to units/ml.

Although examination of the entire area of the settling chamber floor gave a better estimate of plankton concentration and relative proportions, such complete scanning was found to require excessive time for a slight increase in precision. Also, it was necessary to count naturally-occurring units of plankton for the calculation of the Shannon-Weaver diversity index. Filaments of the majority of dominant forms encountered traversed several scans, and it was not feasible to recognize segments of those units which had been counted in previous scans.

The pattern of counting adopted for this study was that of one, two, or four scans perpendicular to each other. A sufficient volume of lake water was added to the chambers to give a total count in excess of 200 units, the level where indexes such as the Shannon-Weaver diversity index tend to stabilize (Tarapchak, 1972). The majority of counts totaled more than 500 units. A total of 59 algal profiles were analyzed, including 40 from Deming, 10 from Arco, and 9 from Josephine.

The unit size of plankton recognized for the purpose of counting and for conversion to biomass was the average of cells or filament length of a given species observed most frequently during the counting procedure. Where cells known to occur naturally in colonial form were found preserved and sedimented in the chamber primarily as unicells (e.g., Synura uvella), the individual cells were counted, and no attempt was made to determine the naturally-occurring colony size. The Lugol preservative caused disruption of such delicate chrysophycean colonies. In contrast, cyanophycean colonies tended to sediment intact. Comparison of both preserved and fresh colonies of Thiopedium rosea from Arco showed that the 4-cell colony is dominant in both instances. Similarly, colonies of Aphanocapsa delicatissima were not affected by the iodine preservative. Appendix II contains a list of the species and unit volumes, as well as the total numbers of each encountered during the three-lake study.

G. Plankton volume was estimated for a unit of each species encountered, with an approximation of the unit to a geometric form having a similar shape and size. In many cases, the algal units are sufficiently complex in form to require the fitting of several geometric forms. For example, Staurastrum species resemble two spheres and several cylinders. Such a method of volume estimation has been negatively criticized, a comparison having been made of volume estimates from both a light microscope and a scanning electron microscope (Lund, 1959). However, errors greater than 20% of the actual unit volume are unlikely. A more serious source of error may arise in the seasonal variation in

unit volume, especially that of filaments which vary greatly in length. However, the present study includes averages of Oscillatoria agardhii v. isothrix filaments from samples collected both at different depths in Deming Lake, and on different dates. The sample average in all cases was within 20% of the unit volume used in all biomass calculations. In contrast, the overall range in unit volumes from the smallest to the largest species is from 15 to 70,000 cubic micra, or nearly four orders of magnitude. Thus, for the purpose of determining relative dominance of species based on total volume, the unit volume estimates suffice as "weights" on the counts, since the errors in them are much less than the wide range in values for all phytoplankton species.

H. Total biomass was estimated with the assumption that the specific gravity of living plankton is exactly 1.000. Previous estimates of actual specific gravity range from less than 1.000 in the case of bloom-forming planktonic blue-greens, to 1.45 in the case of diatoms found in the plankton, such as Fragilaria crotonensis (Hutchinson, 1967). Even a clonal culture of a phytoplankter, e.g., Scenedesmus, contains individual cells and colonies which vary in density with age (Conway and Trainor, 1972). However, it is likely that sources of error other than these are greater. Also, "heavy" diatoms were conspicuously rare in the plankton.

The phytoplankton biomass of an entire study lake was calculated with the relationship:

$$S.C. = \sum_{j=1}^{\Omega} \left(\sum_{i=1}^{S} C_i \cdot f \cdot V_i \right) \cdot W_{z_{2-1}} \cdot 10^{-8}$$

where:

S.C. = Standing crop-biomass, in metric tons

j = A sample within a depth interval

i = A species in a particular sample

Ω = Total number of lake samples in the depth profile

S = Total number of species in sample j

C_i = Number of individuals in species i, sample j

V_i = Volume of a unit of species i, in cubic micra

f = Factor which converts counts in sample j to number/ml

$W_{z_{2-1}}$ = Volume of lake between depths z_1 and z_2, in Hectare-meters

z_1 = Upper depth boundary of sample j, in meters

z_2 = Lower depth boundary of sample j, in meters

The depth boundaries were arbitrarily defined as those depths which were midway between each pair of adjacent sample depths. The surface sample, collected at a depth of from 5 - 10 cm, was given an upper boundary of 0.0 m. The lower boundary of the deepest sample was the bottom depth (17.0 m in Deming, and 10.2 m in Arco). The sampling station was located directly over the deepest point in the lake.

The water volume in any lake element from depth z_1 to z_2 was calculated with the formula for a truncated cone, as suggested by

Hutchinson (1957):

$$W_{z_{2-1}} = (1/3) \cdot (A_{z_1} - \sqrt{A_{z_1} \cdot A_{z_2}}) \cdot (z_2 - z_1)$$

where:

A_{z_1} = Area of the lake at depth z_1, in Ha

A_{z_2} = Area of the lake at depth z_2, in Ha

The area of a lake (A_{z_1}) at depth z_1 was determined by planimetry of isobaths. Areas at depths other than those for which isobaths were available, were estimated by interpolation on a hypsograph. The map of Deming Lake used for all calculations of area was supplied by the Department of Natural Resources, State of Minnesota, and is based on field work carried out in 1964. The map of Arco was drawn by Hibbert Hill, based on his fieldwork carried out in August, 1968, with an electronic depth-sounder and a rowboat. No map of Josephine was prepared.

I. In situ productivity analyses in the lakes were carried out with the oxygen-exchange technique in suspended 300 ml B.O.D. bottles. A pair of light and dark bottles was incubated for 2 to 4 hours at the surface and at half-meter intervals to the bottom of the euphotic zone (∿6m). Dissolved oxygen was analyzed with the azide modification of the Winkler determination.

During the winter of 1967-1968, a plastic-roofed ice-block house was built at the site of incubation. The house provided a snow-free area of constant size. Although the light penetration at the site was artificially large, observations on the relative photosynthetic and respiration rates of the winter populations at

low temperature were made possible. Also, the house was wind-proof, which facilitated handling the glassware at the most extreme ambient temperatures (-40°C).

J. Diversity indexes were calculated from the phytoplankton count data. Several indexes were compared, including S, S/logN, (S-1)/log N, $1-\Sigma P_i^2$, and the Shannon Weaver index calculated both as $N_t!/N_1!N_2!...N_i!$ and as $-\Sigma P_i \log p_i$.

K. Experimental laboratory columns made from polyvinyl cylinders (15 cm x 200 cm) were covered on the bottom to serve as artificial lake columns. The columns had opaque walls, and were made aphotic by capping the upper end. In operation, the columns stood on end in a walk-in cool room with an ambient temperature of 3°±1°C. Lake water was transported as rapidly as possible (~5 hours) from the study lakes, the columns were filled, and a sheet of transparent plastic film was stretched across the surface to prevent vertical mixing from the cool-room circulation fan. An artificial light source of 500 fc (I_o) was provided by a 250 w incandescent bulb above each column. An artificial thermocline was established in the columns by suspending a pair of submersible aquarium-warmers at a depth of 0.5 and 1.0 m.

Samples were taken from the columns at 10 cm depth intervals with a polyethylene siphon tube (inside diam. = 3mm). Incubation periods were from a few days to four weeks. Reversals in light and dark incubation periods were carried out, both at the isothermal 3°C ambient temperature, and in the presence of a thermocline (surface temperature = 15°C).

RESULTS

A. PHYSICAL-CHEMICAL PROFILES

TEMPERATURE PROFILES

During each spring from 1968 through 1971, the weather following ice-melt was clear, calm, and warm. The surface water of the study lakes warmed quickly, and shallow thermoclines developed between the surface and 3 m. By June, the thermocline in Deming and Josephine descended to 3-5 m, and in Arco to 5-7 m. (The deeper thermocline in Arco cannot be explained by invoking wind mixing as the lake is smaller, has a larger relative depth, and is more protected by forested slopes than is either Deming or Josephine. Deeper penetration of sunlight and absorption by the deeper algal strata is here suggested as an explanation for the phenomenon.)

Secondary thermoclines often develop in the upper meter of the lakes, with water temperature at times approaching 30°C. Below 7m, the temperature remains at 4.5±1°C year-round. The seasonal pattern of isotherms is similar in the three lakes, in general being a slow descent of the isotherms (in the range 6° to 22°C) throughout the summer (Figs. 4, 5, 6).

A considerable variation in temperature gradient per unit depth interval occurred in the region of the thermocline (Figs. 7, 8, 9). The pattern of thermal microstructure is not unlike that observed in Loch Ness (Simpson and Woods, 1970), although gradients as high as 2.2°C/10 cm were recorded during this study, an order of magnitude greater than those found in Loch Ness. The locations

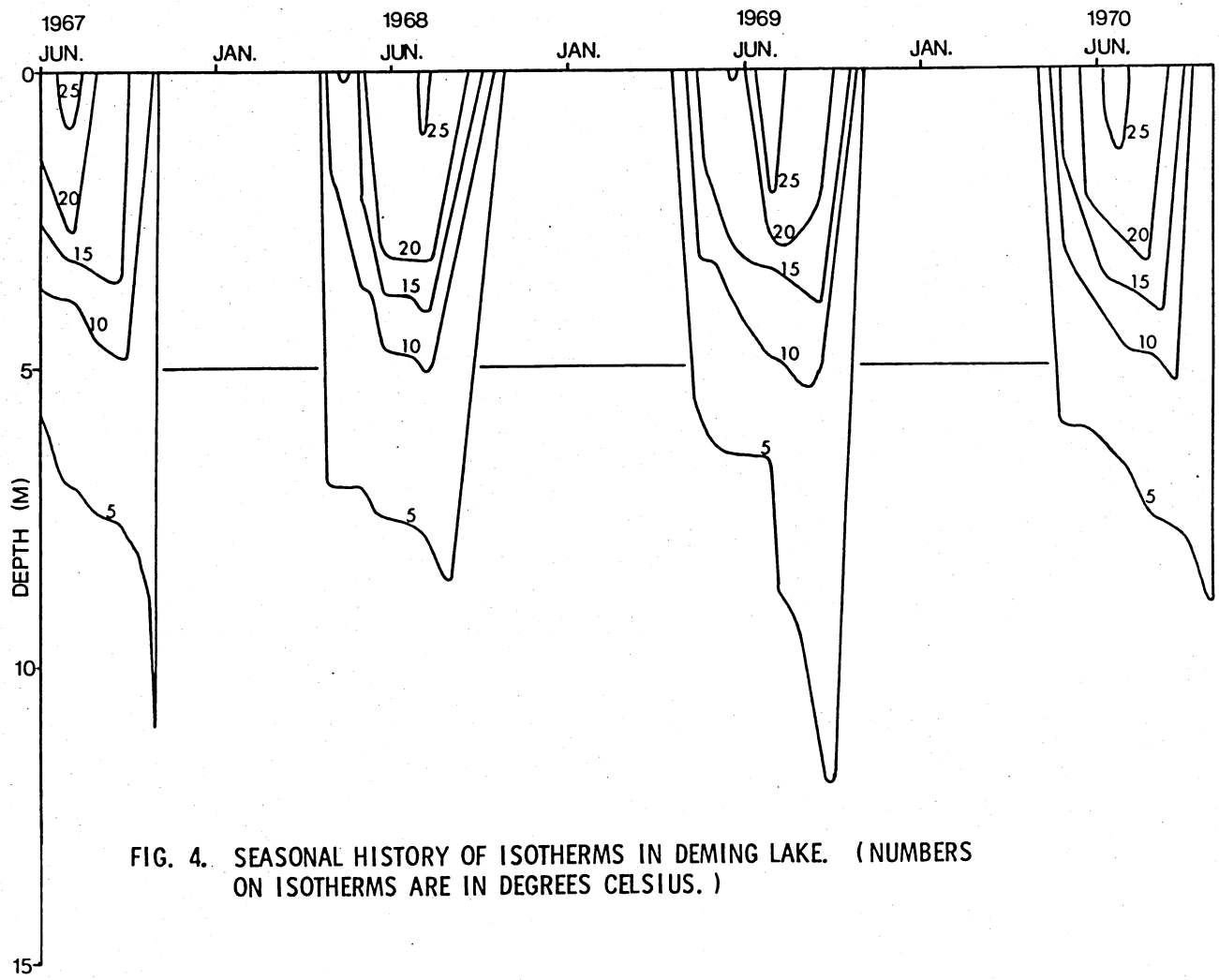


FIG. 4. SEASONAL HISTORY OF ISOTHERMS IN DEMING LAKE. (NUMBERS ON ISOTHERMS ARE IN DEGREES CELSIUS.)

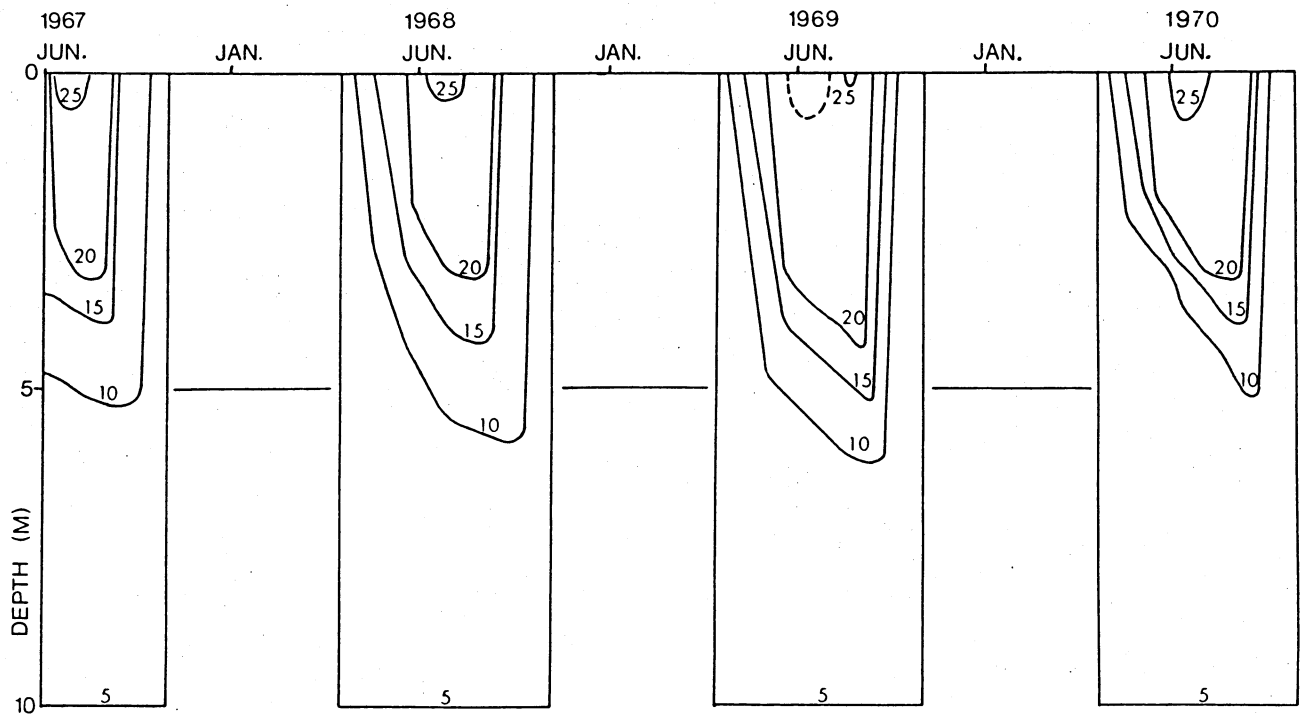


FIG. 5. SEASONAL HISTORY OF ISOTHERMS IN ARCO LAKE (NUMBERS ON ISOTHERMS ARE IN DEGREES CELSIUS.)

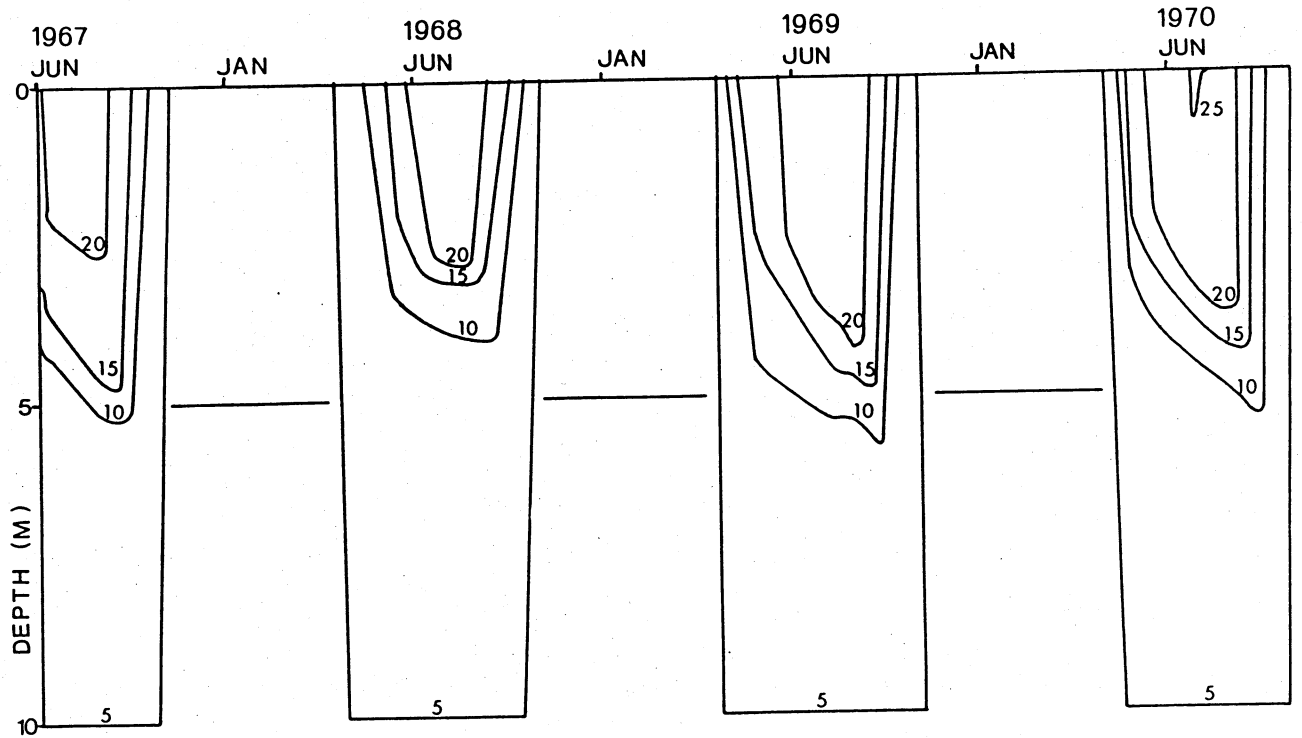


FIG. 6. SEASONAL HISTORY OF ISOTHERMS IN JOSEPHINE LAKE. (NUMBERS ON ISOTHERMS ARE IN DEGREES CELSIUS.)

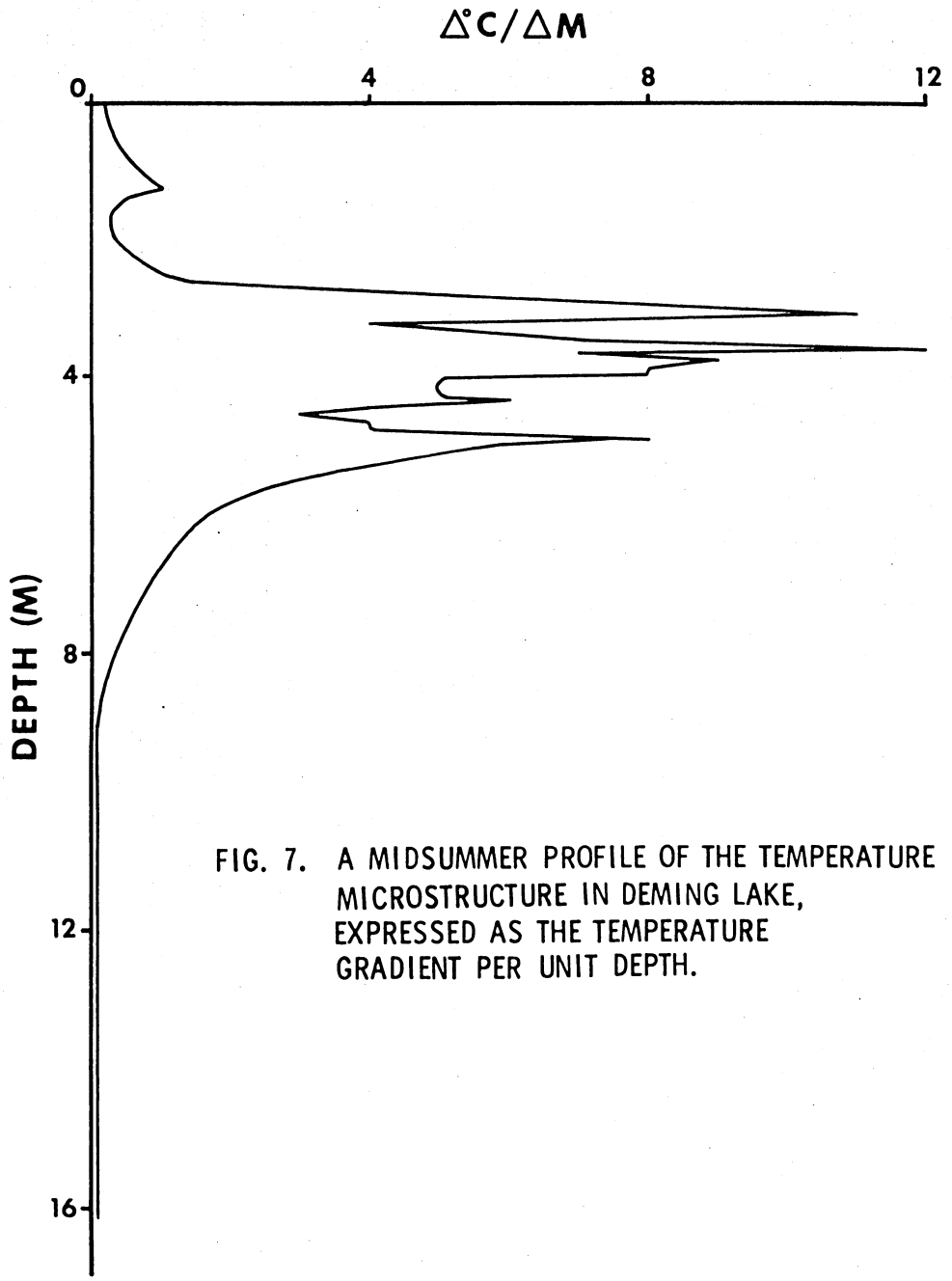


FIG. 7. A MIDSUMMER PROFILE OF THE TEMPERATURE MICROSTRUCTURE IN DEMING LAKE, EXPRESSED AS THE TEMPERATURE GRADIENT PER UNIT DEPTH.

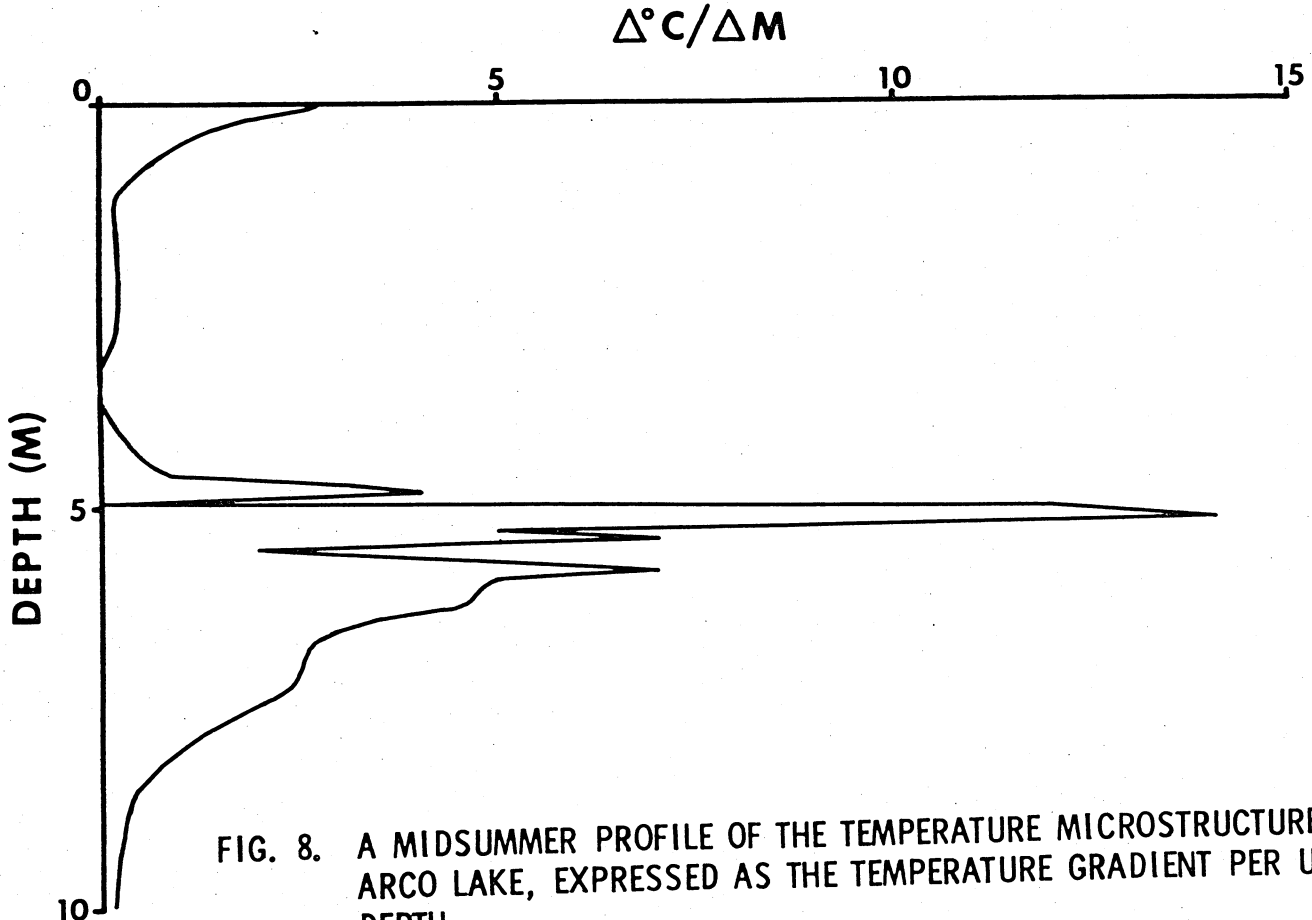


FIG. 8. A MIDSUMMER PROFILE OF THE TEMPERATURE MICROSTRUCTURE IN ARCO LAKE, EXPRESSED AS THE TEMPERATURE GRADIENT PER UNIT DEPTH.

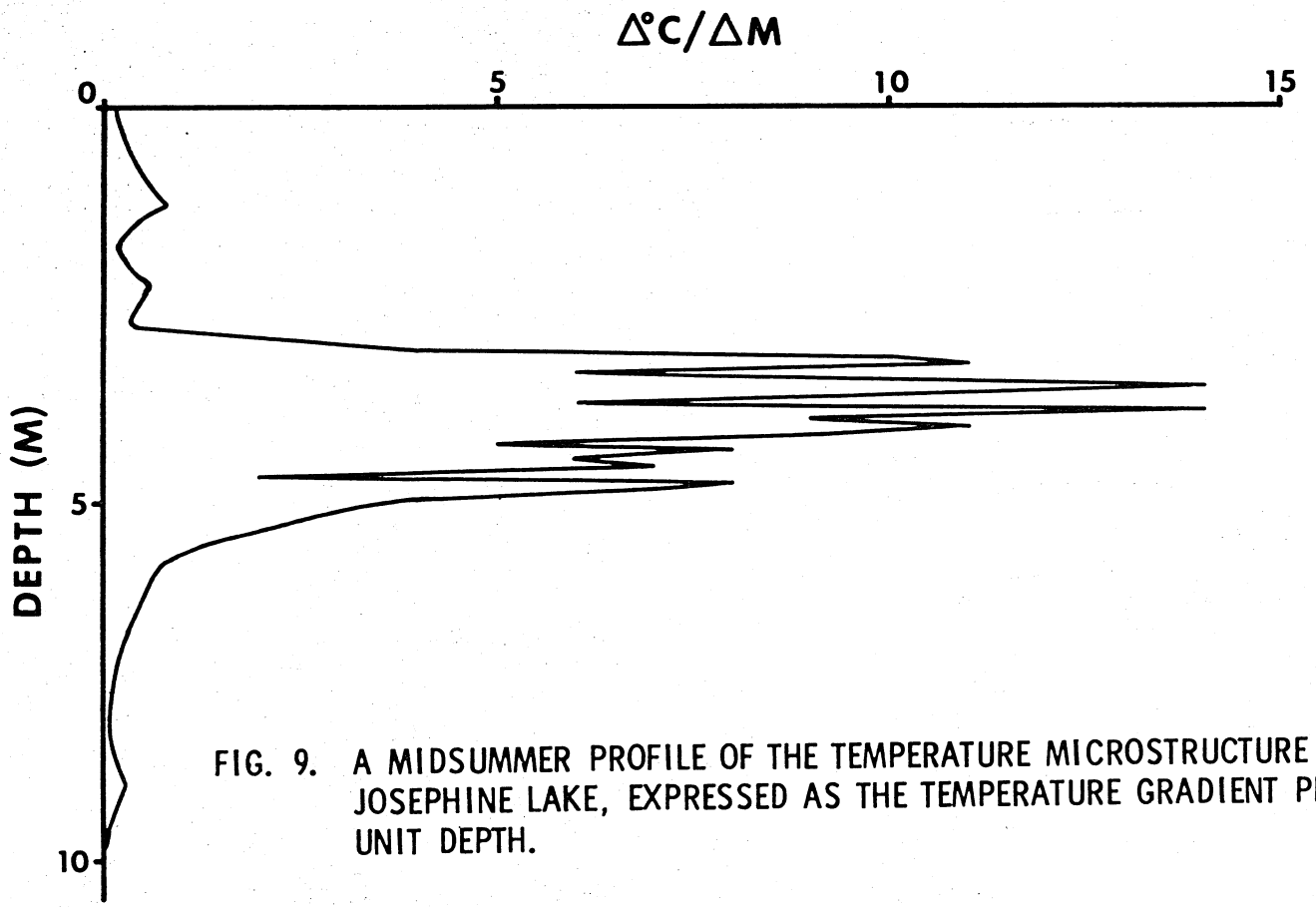


FIG. 9. A MIDSUMMER PROFILE OF THE TEMPERATURE MICROSTRUCTURE IN JOSEPHINE LAKE, EXPRESSED AS THE TEMPERATURE GRADIENT PER UNIT DEPTH.

of the microstructures of temperature, optical density, and phytoplankton in the study lakes are similar.

LIGHT

Light absorption tended to increase in the study lakes during the summer. Absorption was found to be greatest in the region of the thermocline. Plots of the log of the light intensity vs. depth tend to bend upward rather than being linear (Fig. 10). There was little change in the seasonal pattern of light extinction in Deming from 1968 - 1970, (Fig. 11) while the extinction in the surface waters of Josephine increased during the 3 year period (Fig. 12).

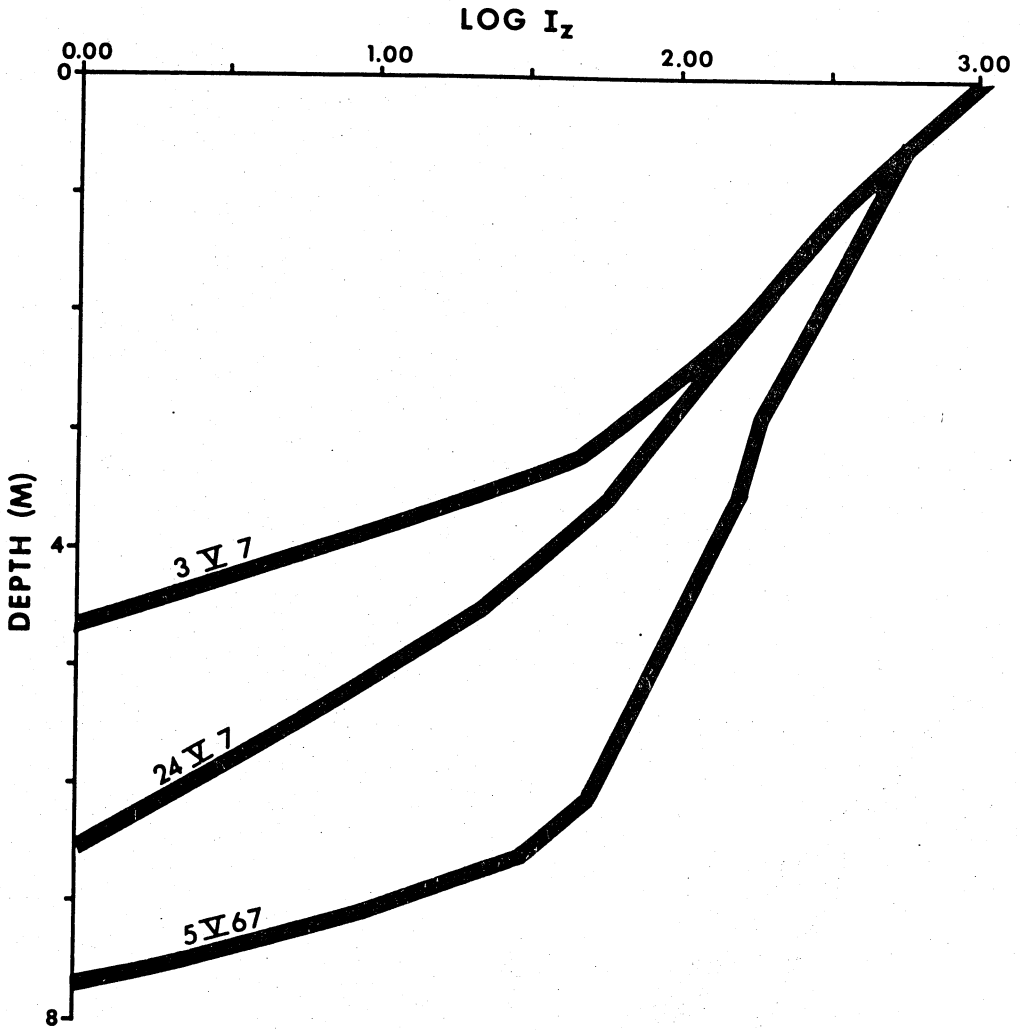
OPTICAL DENSITY

The O.D. profiles in the three lakes were complex, with a microstructure that slowly changed throughout the year. Sharp gradients in O.D./unit depth were recorded, the highest values being more than 2.000/10 cm. The profiles can be characterized by a single sharply-delineated maximum within or below the metalimnion, accompanied by lesser peaks above and below. Frequently, there was no apparent increase in O.D. in the bottom waters. The principal peak was usually located between 4-5 m in Deming and Josephine, and between 6-7 m in Arco.

Annual repetition of pattern in the late-summer profiles was was observed from 1968-1971 in all three lakes, with the exception of the 1970 profiles in Arco. The following discussion is based on the set of optical density profiles (Appendix 1).

Variation of the profiles in Deming was recorded during all seasons. In January, a maximum in O.D. developed against the

FIG. 10. THREE LIGHT PROFILES IN ARCO LAKE, SHOWING THE PROGRESSIVE INCREASE IN LIGHT ABSORPTION DURING THE SPRING.



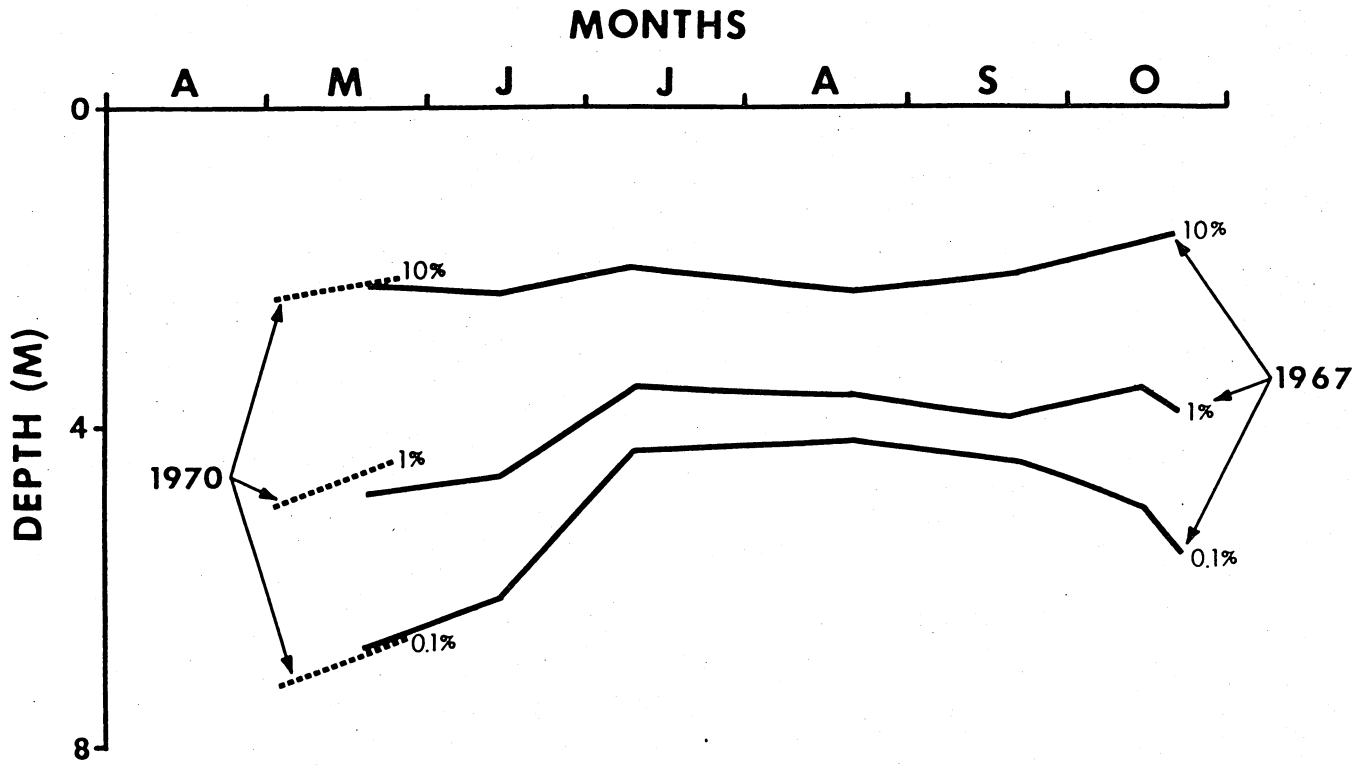


FIG. 11. SEASONAL VARIATION IN THE 10%, 1%, AND 0.1% LIGHT ISOPLETHS IN DEMING LAKE.

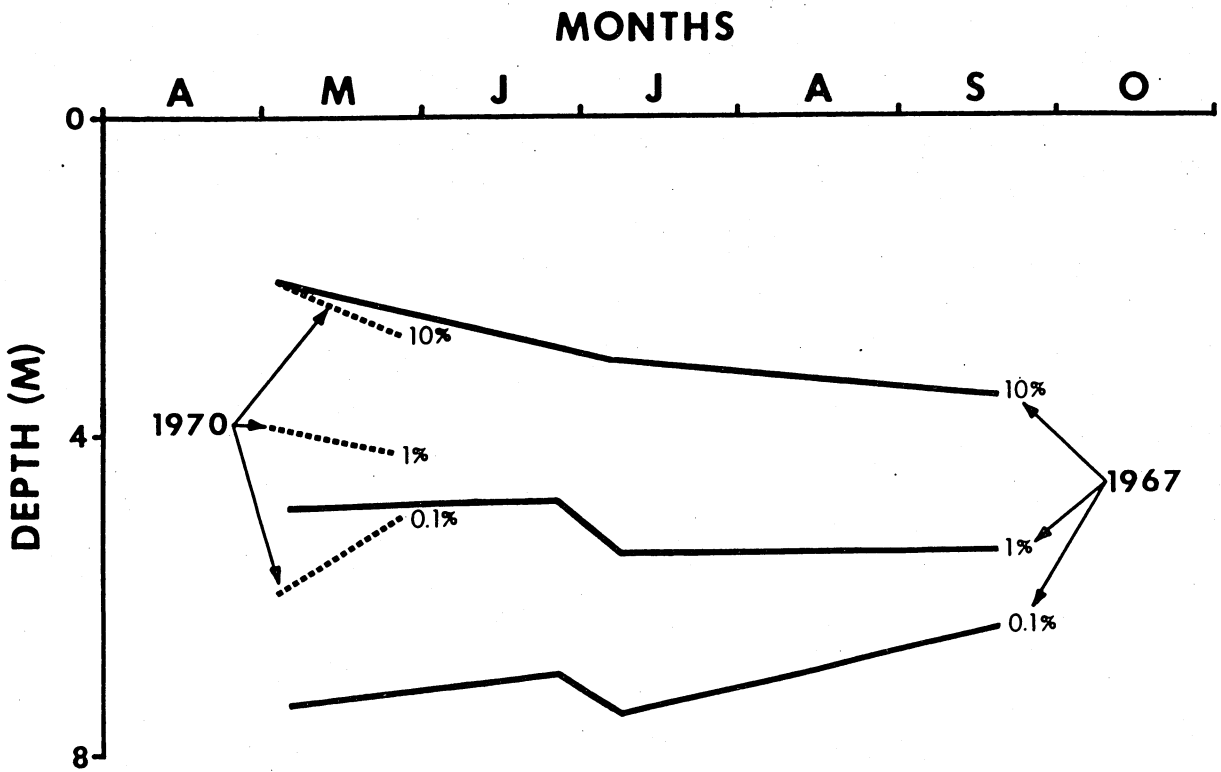


FIG. 12. SEASONAL VARIATION IN THE 10%, 1%, AND 0.1% LIGHT ISOPLETHS IN JOSEPHINE LAKE.

underside of the ice cover. As the ice began to melt in early April, the maximum O.D. descended to more than a meter beneath the ice, and a layer of clear meltwater formed above the peak. After ice-melt, the O.D. peak continued to descend to a depth of 5-6 m. During May and June the peak became more intense and more sharply delineated while remaining near 5 m. A smaller peak developed at 2-3 m. During July and early August, the 5 m peak continued to grow. The upper peak also became more intense at this time, gradually descending as the lower peak rose slightly; the two sometimes merged. As the surface waters cooled in early September, mixing of the upper 3 m of water erased the upper O.D. peak. By mid-October, the lower peak also disappeared, and the O.D. of the surface water increased. The profile was nearly uniform to a depth of 10 m at the time of maximum mixing (late October). After ice formation, the O.D. in the upper 10 m decreased while a relatively small peak remained at 11-13 m. By early January, the winter peak under the ice developed.

A survey of several lakes in the vicinity of Itasca State Park showed the presence of microstructure in O.D. in every one, no two profiles being alike (Baker and Brook, 1971). Although O.D. gradients were sharpest in the smaller lakes, the presence of a microstructure even in Lake Itasca (which has been observed to mix completely during July storms) confirms that the phenomenon is not unique to wind-protected lakes.

Metalimnetic O.D. peaks were associated with high temperature gradients of greater than 0.1°C/10 cm. The hypolimnetic O.D. peak in Arco, in contrast, was located at a depth where the

temperature gradient was much less than 0.1°C/10 cm, but where a positive gradient in conductivity was found. In every case, a minimum of vertical mixing at the time of sampling was implied.

The uniformity of the O.D. profiles across the lake (Deming) was determined at a series of stations at 25 m intervals traversing the lake (Fig. 13).

Conductivity and pH profiles in the study lakes both showed the presence of a microstructure in the metalimnion. Conductivity dropped to a minimum value of 45-50 micromhos at 4.5 m in Deming, as much as 20 micromhos/cm lower than the values at 4.0 m and 5.0 m. The pH was at a maximum value of 11.3 at 4.5 m, although only 8.0 at 4.0 m, and bounded at 5.0 m by a sharp gradient, to a pH of 6.5. Hydrogen ion has the highest activity of any dissolved ion, thus variations in its concentration cause greater variations in conductivity than those of other dissolved substances. The low conductivity and high pH at 4.5 m may have been a consequence of this relationship.

Dissolved oxygen profiles in all three study lakes during the summer were strongly positive-heterograde (Ruttner, 1952); the peak value often exceeded 20 ppm, and on occasions values of higher than 35 ppm were encountered (Fig. 14). Steep concentration gradients bound both the upper and lower depths of the peak, often limiting it to a 60 cm interval. A secondary peak occasionally occurred at shallower depths, while anoxic water with the distinct odor of hydrogen sulfide invariably was found beneath the peak in oxygen.

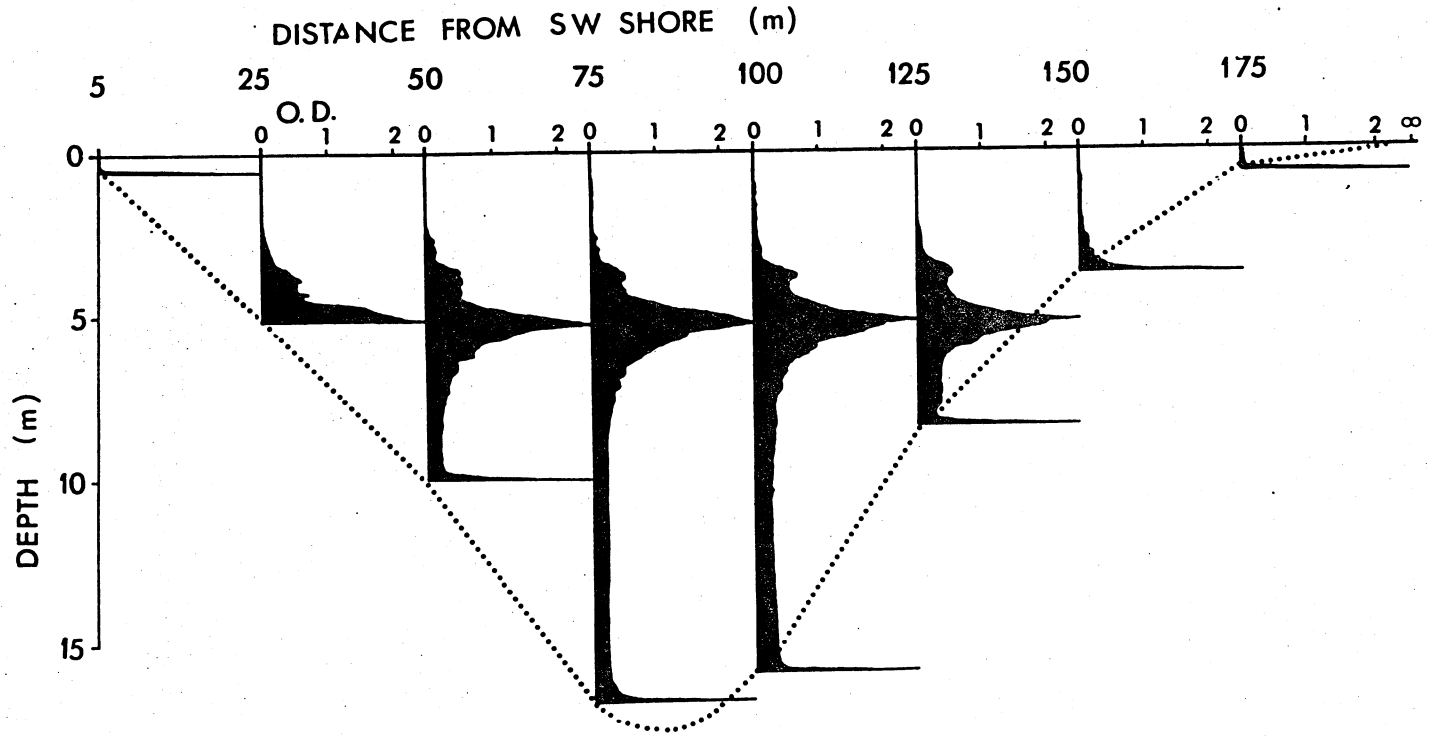


FIG. 13. OPTICAL DENSITY PROFILES ALONG A TRANSECT ACROSS DEMING LAKE.

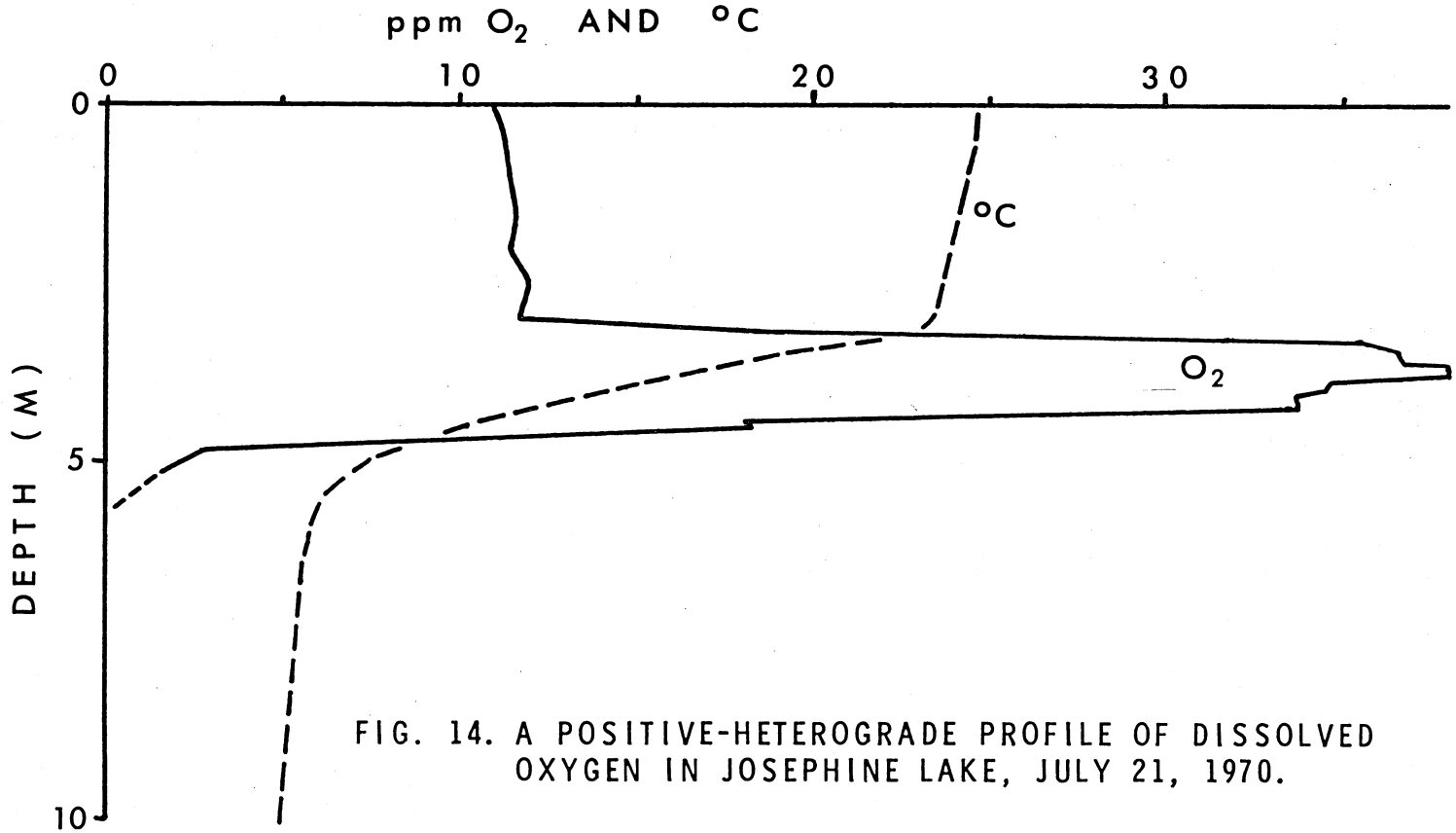


FIG. 14. A POSITIVE-HETEROGRADE PROFILE OF DISSOLVED OXYGEN IN JOSEPHINE LAKE, JULY 21, 1970.

Fall mixing carried oxygen to the bottom waters in Josephine each year, while the lowest 2 m in Arco were never oxygenated. Only in 1967 was a measurable concentration of oxygen found below 12 m in Deming. However, the bottom waters returned within a few days to an oxygen deficient condition. It is possible that oxygenated water reached the mud surface in late October during 1968-1971, although none was present below 10-12 m in those years as late as October 25, 1969 or November 7, 1970. Ice formed on Deming within a week of those dates, after which event mixing due to wind must have decreased. Density differences between depths was at a minimum during that time, however, and it is possible that residual currents carried oxygen to the bottom waters. Deming was intermediate between Josephine and Arco with respect to the degree of oxygenation of the deepest muds. None of the lakes mixed sufficiently during spring to oxygenate the bottom waters. Expressed as a percentage of the total lake volume, approximately 90% of the lake water mixed in spring, while 100% of Josephine, 95% of Deming, and 97% of Arco were well mixed in the fall. Since incomplete mixing is a criterion, Arco is definitely meromictic, and Deming is at least oligomictic.

Less than 5% of the volume of Deming and Arco remained stagnant. The portion of water from between 5 and 10 m in each lake that did mix, carried with it to the surface the nutrients which during the summer had increased below the epilimnion. The remaining nutrients locked within the small volume of completely stagnant bottom water were very concentrated (see Introduction).

Oxygen concentration dropped during the winter to very low levels, with at most 2 ppm present even at the surface. Anoxic, sulfide-rich water was found at all depths below 3 m (under the ice).

B. STRATIFICATION OF INDIVIDUAL SPECIES DURING LATE SUMMER

Algal strata, here defined as those measurable peaks in abundance along the depth profile, were found to occur in each of the study lakes. The strata were most pronounced during July and August, although some were present throughout the year.

Optical density profiles obtained with the transmissometer indicated the existence of a microstructure at the scale of millimeters in the depth column. However, resolution of the microstructure of individual algal strata was limited by the sampling technique, collections having been made at 20 cm intervals. The minimum measurable thickness of a stratum can be no less than twice the sampling interval (here, 40 cm). Frequently, the concentration of a particular species which formed very thin strata, e.g. Dinobryon divergens, was high in a single sample, yet nearly or completely absent in the immediately adjacent samples. Such strata, then, were thinner than 40 cm.

In contrast to the pronounced strata characteristics of the majority of species, there were a few species, e.g. Synedra acus, that frequently were present in a nearly uniform concentration throughout the depth column.

Many species tended to form a single dense stratum within their profile, and tended to be dominant within their profile relative to the entire phytoplankton assemblage. (This did not

hold in the case of some stratified but relatively rare species.) Examples include Oscillatoria agardhii v. isothrix and Anabaena cylindrica (Figs. 15, 16). Of those species which formed more than one stratum, e.g. Cryptomonas erosa and Oscillatoria redekei (Figs. 17, 18) it is possible that two species were lumped. C. erosa is very similar morphologically to C. ovata, as is O. redekii to O. trichoides. In like manner, the differences may have been at the level of subspecies.

The pattern of distribution appeared to be species-specific. Oscillatoria agardhii v. isothrix retained a similar profile shape throughout the summer in Deming (see Section D below). Other species of Oscillatoria including O. redekei, were quite unlike O. agardhii v. isothrix in their pattern of distribution. Differences of this type were also found among the Anabaena species.

When the stratified species are grouped into those which form predominantly epilimnetic strata there is little taxonomic relationship among the members of the group. The same is true for the metalimnetic group and the hypolimnetic group. An implication is that similar strategy or environmental adaptation has developed in very diverse groups of algae.

The profiles of individual species were compared in several ways:

1) the absolute concentration of individuals per ml at each depth
2) the absolute volume per ml at each depth

FIG. 15. ABUNDANCE PROFILES OF OSCILLATORIA AGARDHII. V. ISOTHRIX IN DEMING LAKE ON AUG. 6, 1970. (NOTE ESPECIALLY THE DIFFERENCE IN PROFILE SHAPE, DEPENDENT ON THE TYPE EXPRESSION OF ABUNDANCE.)

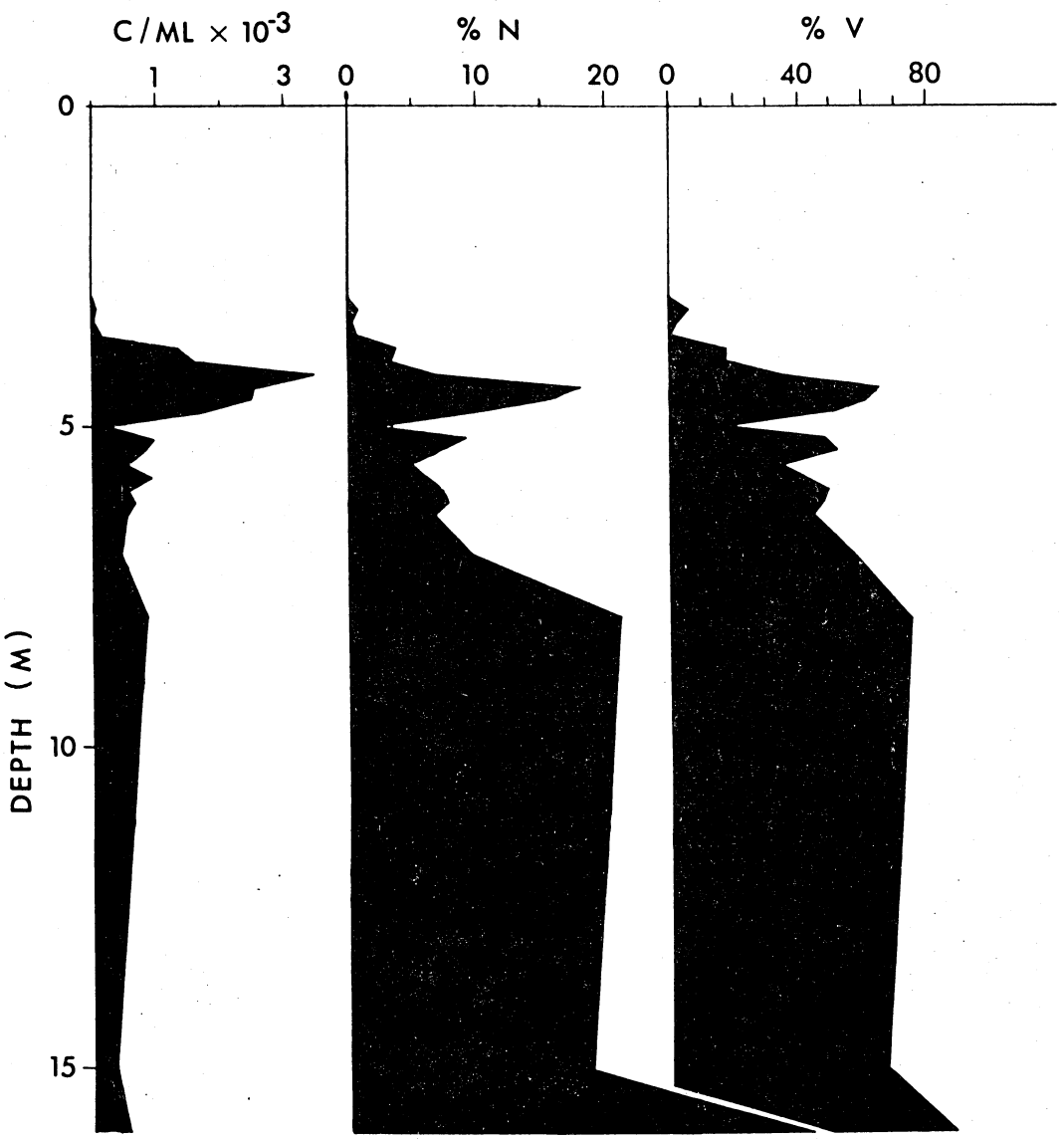


FIG. 16. ABUNDANCE PROFILES OF ANABAENA CYLINDRICA IN DEMING LAKE ON AUG. 6, 1970.

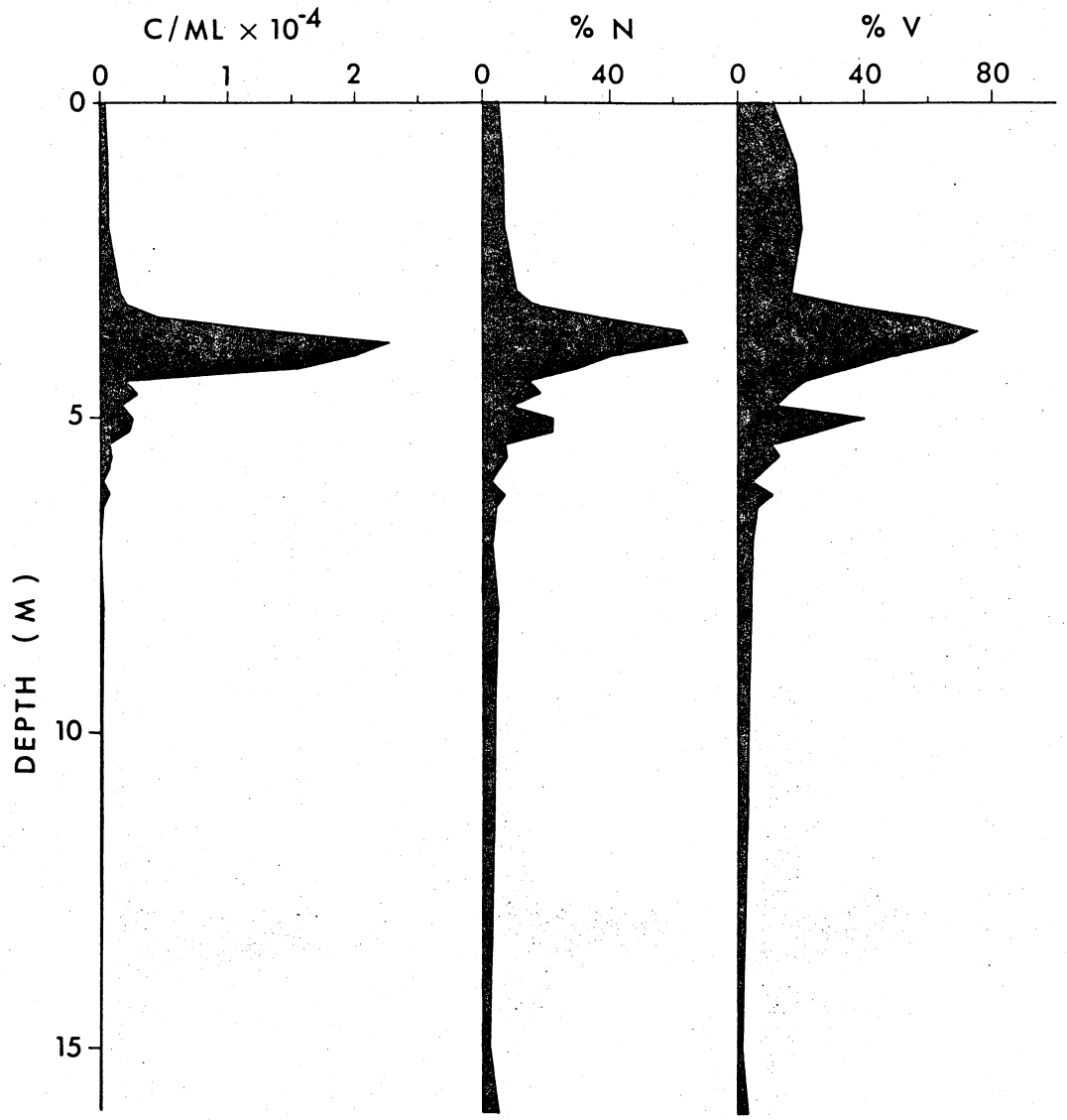


FIG. 17. ABUNDANCE PROFILES OF CRYPTOMONAS EROSA IN DEMING LAKE ON AUG. 6, 1970.

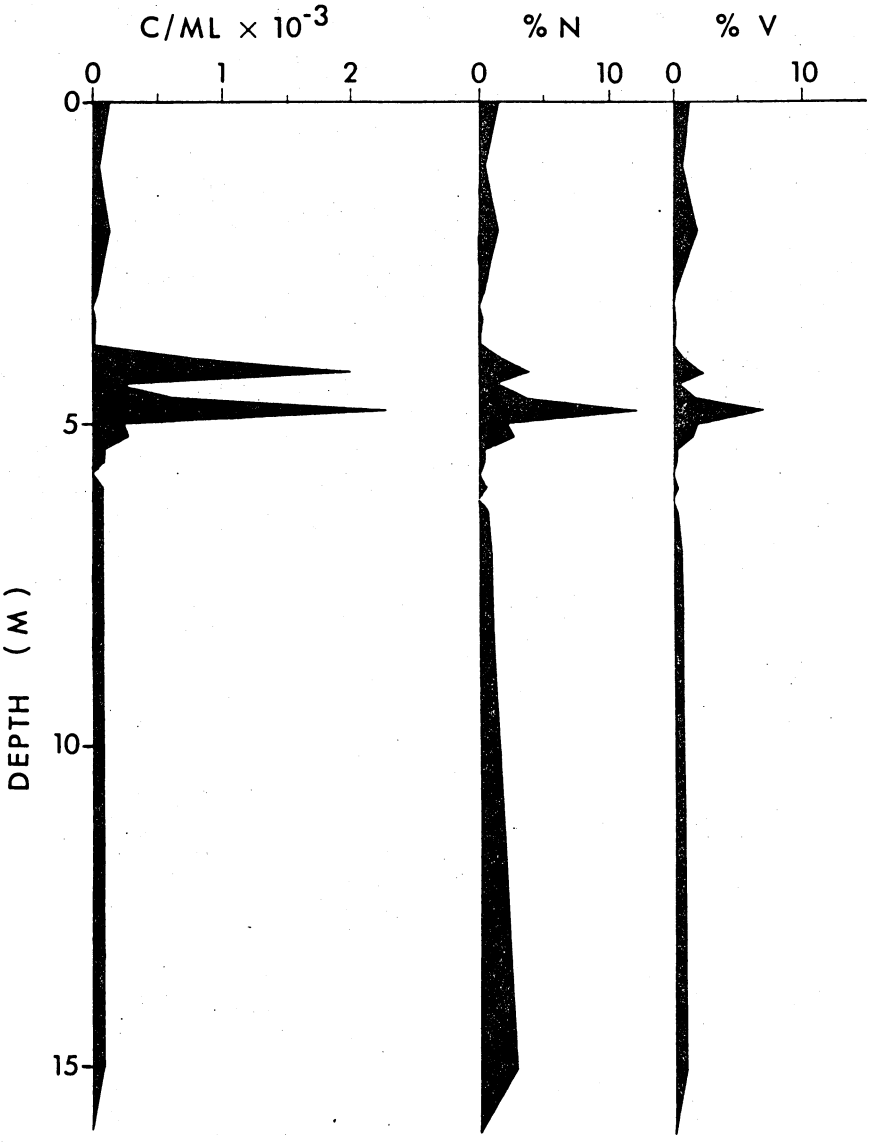
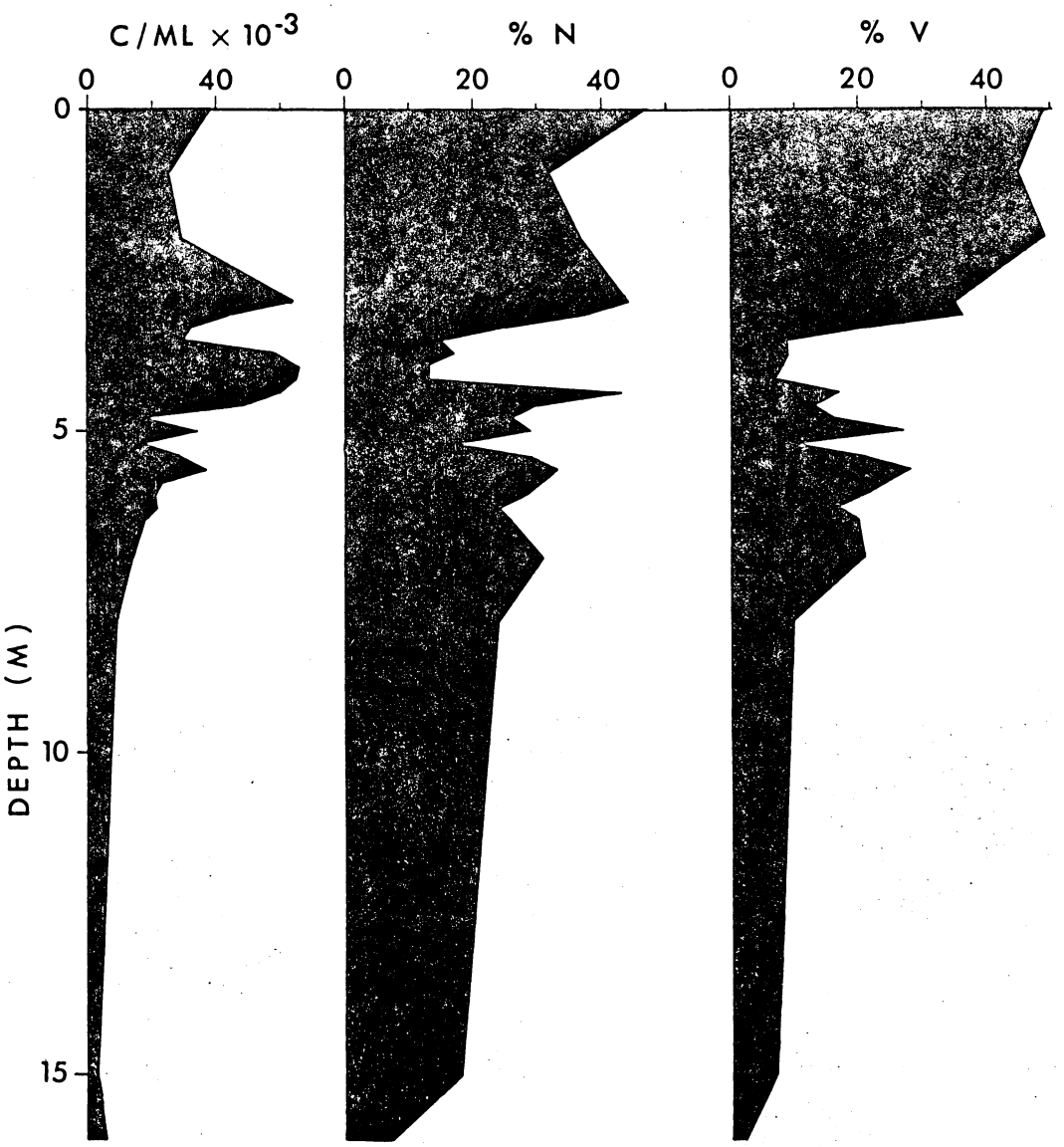


FIG. 18. ABUNDANCE PROFILES OF OSCILLATORIA REDEKII IN DEMING LAKE, AUG. 6, 1970.



3) the percentage at each depth of the number of individuals of all species

4) the percentage at each depth of the volume of all species

5) the percentage at each depth of the maximum number of individuals of the same species found anywhere in the column.

Each of the expressions produces a differently-shaped profile, and has a different meaning which requires a particular interpretation. The majority of published reports of phytoplankton distribution and concentration include only expression 1, the number per ml (or per liter). The main advantage of the expression in this study is that it is the only one of the above five that permits a comparison with other published data.

Expression 2, the volume per ml of each species, carries much more information about the species. It includes both numbers per ml and average volume of the individual plankter. The advantage of this expression is that it permits an approximation of the total biomass of each species. With regard to biomass, rapid growth in small numbers of small plankters can be insignificant relative to slow growth of large numbers of large plankters.

Expression 3, the relative number of each species, permits an estimate of diversity based on relative abundance, e.g., the Shannon-Weaver diversity index. Also, a similar expression can be readily obtained from published reports on algal abundance.

Expression 4, the relative volume of each species, permits an estimate of the nutrient and metabolite content of each species relative to the entire community.

Expression 5, the relative column abundance, compares the concentration of a species at each depth relative to its maximum abundance in the depth column. The expression permits a comparison of the profile shapes of two or more species, even when the maximum abundance of the various species is very different. For example, the profile of a very rare species appears to be without strata when graphed on the same scale as that of an especially abundant species. Expression 5 normalizes the two profiles, so that the maximum abundance of the two species is the same. The normalization brings out the complexity of the rare species' profile. The two species may stratify in similar manners. If so, they may be reacting in similar ways to environmental gradients throughout the depth profile.

C. ORDINATION OF SPECIES IN DEPTH

During July and August, when the perennial populations reached their maximum degree of stratification, a distinct and consistent relationship was observed. Although the vertical distance or depth interval between their strata varied, the strata of the dominant species were arranged in an unchanging order from the shallowest to the deepest.

Nine species, each being one of the nine most encountered species, and together representing more than 80% of all units counted, were selected for comparison. Four of the species were dominant in all three lakes, two were in two, and three occurred in significant numbers in only one lake (Table 1).

Most of the nine dominants were found throughout the depth column, others at times were more restricted in their distribution.

TABLE 1. Ordination in depth of the nine most dominant species encountered, and the range in temperature within their strata in the three study lakes.

SPECIES	DEMING	ARCO	JOSEPHINE
Lyngbya limnetica	19-27°C		
Oscillatoria amphibia	18°C		
O. redekei	10-15°C	13-21°C	12-20°C
Anabaena cylindrica	10-15°C	11-15°C	12-20°C
O. agardhii v. isothrix	6-12.5°C		5.5-8°C
Cryptomonas cf. erosa	5.7-10°C	10-11°C	6-10°C
Ankistrodesmus falcatus	5.5-7°C	11°C	6°C
Thiopedia rosea[1]		5.2-8°C	5-5.5°C
Arthrospira abbreviata		5.6°C	

[1]Possibly Merismopedia trolleri.

All formed sharply delineated peaks, the location of which is designated as the depth of the stratum.

The species ordination was persistent from mid June through August. As the surface temperature increased through the summer, the temperature within the upper strata increased by several degrees, while that in the deeper strata increased only slightly or not at all. By late August, four strata were warmed to greater than 10°C, and the rest remained in cooler water. Among the cold-water forms, there was a tendency for those common to all three lakes to stratify at higher temperatures in Arco than in Deming and Josephine. The warm-water forms had remarkably similar ranges in all three lakes.

D. SEASONAL CHANGES IN SPECIES DISTRIBUTION

Most of the species populations encountered during the study were perennial. Every perennial population formed strata which persisted throughout the year with the exception of brief periods of a few days during spring and fall when the upper few meters in each lake became isothermal. Summer profiles differed from winter profiles, and there were transitional stages between them.

Several species that were most abundant in August had already developed rudimentary strata within a few days following the final ice-melt in late April. The initial strata were always located at depths near the surface, at a high light intensity. Subsequently, the strata settled into greater depths, reaching their greatest depth by late June.

During July and August, the deepest strata within the metalimnion and hypolimnion reversed their direction of migration,

moving upward during the two-month period by more than 1 m and following the 1% I_0 light level or less. A similar reversal is suggested in the data of Northcote and Halsey (1969) who used high-frequency echo-sounding on some meromictic lakes in British Columbia (see esp. lakes Lyons and Mahoney). The shallower strata tended to continue their downward migration during the same time period. In every instance, however, the densest stratum developed during August. With the cooling trend during September and October, the surface water mixed into the metalimnion. The deeper strata were progressively eliminated and several deep-water forms suddenly appeared at the surface. Only the deepest strata persisted intact into late October.

Ice formed during November. The first winter strata developed directly beneath the ice in December, and these increased in concentration until ice-melt in April. Those species which formed the deepest strata during summer also formed the densest winter strata.

The predominant species forming epilimnetic and shallow metalimnetic summer strata was Oscillatoria redekei, present in large numbers up to 50,000 fil./ml in Deming, Arco, and Josephine. Its abundance however was erratic, as it formed surface blooms of various densities in different years in different lakes.

The blooms developed during June, giving the lake waters a muddy appearance for two weeks or longer. Although the lake had an appearance of greater clarity after the disappearance of the surface bloom, O. redekei became abundant as a very dense stratum at the base of the epilimnion by early July. Strata of O. redekei

were present in all three study lakes at this time. The shallow strata were the first to disappear as vertical mixing began in September. In the winter this species formed a surface stratum.

The predominant metalimnetic species in Deming and Josephine, while almost entirely absent from Arco, was Oscillatoria agardhii v. isothrix. It was predominant throughout the year in Deming and Josephine, forming a concentrated surface stratum during the winter. The species was quite consistent in its distribution and population development each year (Figs. 19, 20, 21). There were no filaments present during much of the summer throughout the epilimnion and upper metalimnion, while the filaments within the 4-6 m stratum reached a concentration of 50,000/ml (a fresh weight of 283 mg/l). Shortly after ice-melt, the majority of O. agardhii v. isothrix filaments descended rapidly to a depth of 5.5-6m. The population increased throughout June - August, and the stratum became increasingly more sharply defined. It gradually migrated upward nearly 1.0 m during the summer. By mid-August, the peak in abundance occurred at 4.6 m. It was not until early October that the effects of vertical mixing reached the O. agardhii v. isothrix stratum, at which time the stratum was suddenly eliminated, and filaments in great concentration appeared in the surface waters. Had not in-depth sampling been done, the sudden surface accumulation of this deep-water species would have been mistaken easily for a fall blue-green bloom. In fact, the biomass in the lake of this species had been declining since August. The winter population of O.

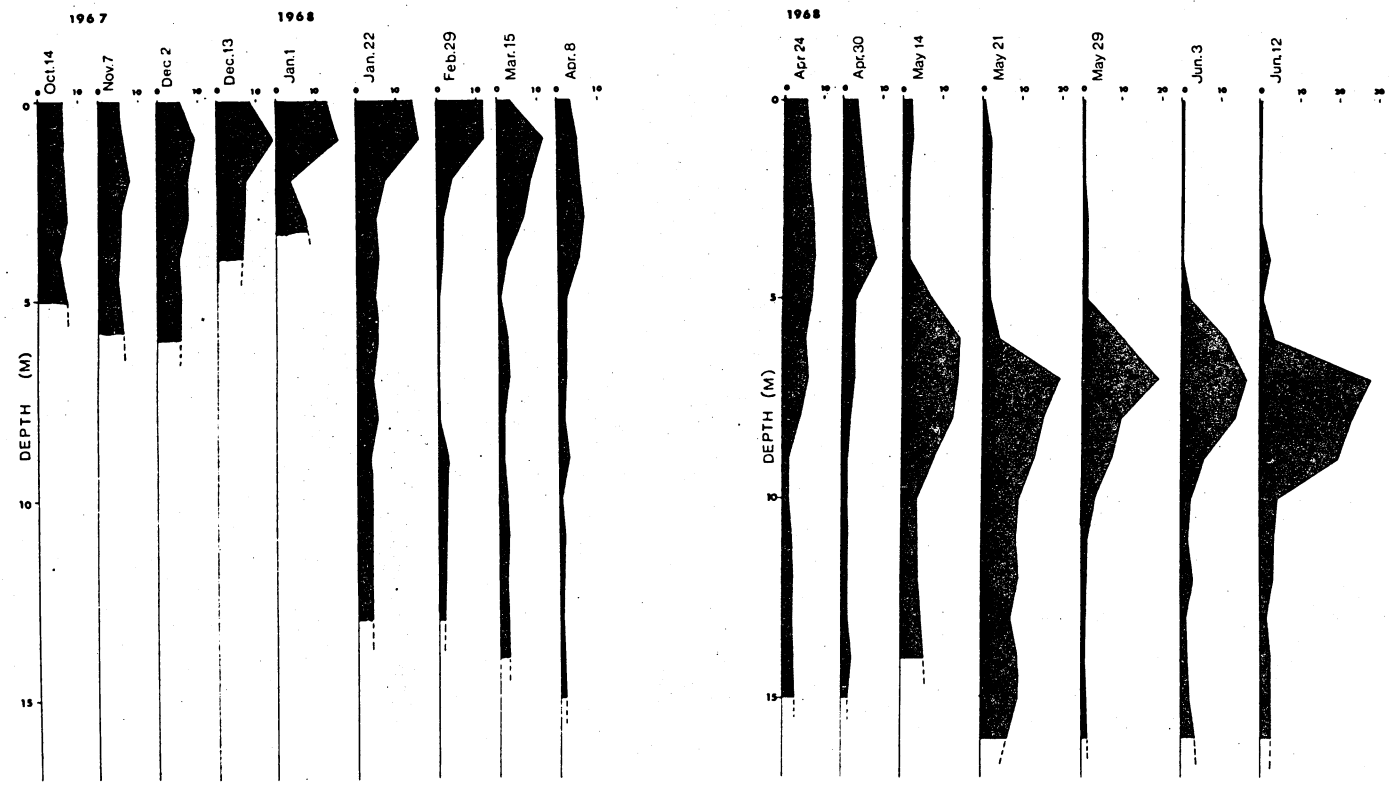


FIG. 19. ABUNDANCE PROFILES OF OSCILLATORIA AGARDHII V. ISOTHRIX IN DEMING LAKE, 1967 AND 1968. (IN THOUSANDS OF FILAMENTS PER ML)

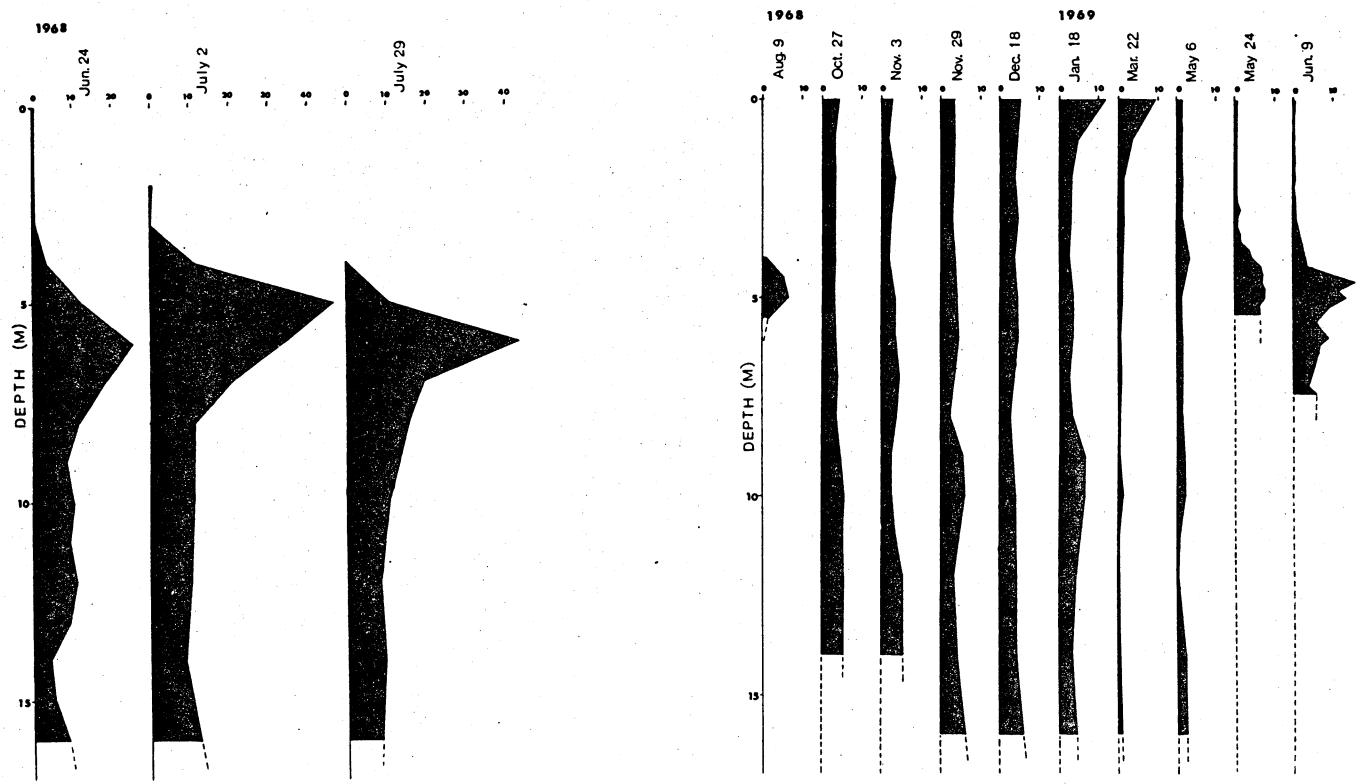


FIG. 20. ABUNDANCE PROFILES OF OSCILLATORIA AGARDHII V. ISOTHRIX IN DEMING LAKE, 1968 AND 1969.

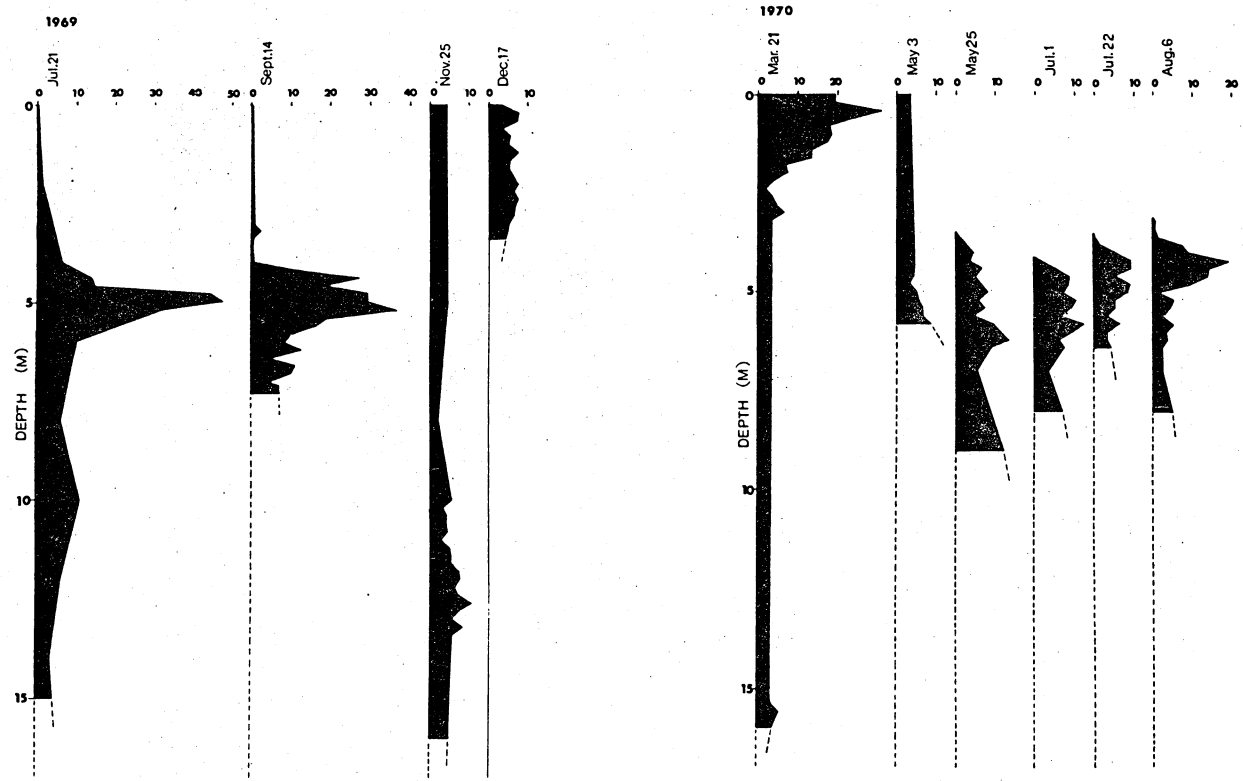


FIG. 21. ABUNDANCE PROFILES OF OSCILLATORIA AGARDHII V. ISOTHRIX IN DEMING LAKE, 1969 AND 1970.

agardhii v. isothrix again increased to a maximum prior to ice-melt in April.

In Arco, the predominant metalimnetic species was Anabaena cylindrica. The alga was also abundant in the metalimnetic community of Josephine, and partially replaced O. agardhii v. isothrix in Deming during 1970. Anabaena cylindrica formed strata later in the summer than did O. agardhii v. isothrix, and at a shallower depth. It was never present in great numbers during the winter, and was the species showing the greatest seasonal variation in total biomass. It was a late-summer form, occurring in large numbers only in August and September.

The predominant hypolimnetic species was either the cyanophycean Merismopedia trolleri, or more probably the purple photosynthetic bacterium Thiopedia rosea, present in the greatest concentration in Arco during the summer (more than 400,000 colonies/ml. within the stratum). It was also important in the hypolimnion of Josephine, but was rarely found in Deming. During the summer, T. rosea disappeared from the upper 5 m of Arco and Josephine, at the same time increasing its total-lake biomass (being entirely restricted to a well-defined stratum in the hypolimnion). Within the Thiopedia stratum, the lake-water was always anoxic and sulfide-rich. Often the great concentration of this species gave a distinctive milky-green cast to the samples, and occasionally a red-purple color. Although this highly-pigmented species must have been photosynthetically active, no test of its activity was carried out other than the observed build-up of its population within the hypolimnion. During a three-week period

after ice-melt, Thiopedia rosea descended to a depth of 7.5 m where its numbers increased. Throughout the summer an upward migration occurred, shifting the stratum by mid-September to 6.5 m. Even at this depth, the vertical mixing in October was not sufficient to bring the species to the surface. Instead, the stratum persisted intact, and gradually descended to near the bottom sediments (9.5 m). However, in December and January a sharply-defined winter surface bloom developed under the ice. Accompanying T. rosea was a layer of detrital material on the underside of the ice. At this time the surface water was very turbid, and contained flocculent material. Sections of bottom mud had become buoyant, broken loose from the bottom, and floated upwards. Bubbles, presumably formed under the anoxic conditions near the bottom of the lake, were found trapped in the mucilaginous matter floating at the surface. It is assumed that the T. rosea colonies (as well as other planktonic organisms) were transported passively from the mud-water interface to the surface, where, in the presence of light and enriched surface waters, they were able to photosynthesize and form the winter bloom.

Among perennial populations, those which formed the deepest summer strata tended to form the largest winter populations, and throughout the year such populations grew best under low-light, low-temperature, and high-nutrient conditions.

The one dominant summer form which was rarely present in winter was Anabaena cylindrica. It has not been possible to determine where it over-wintered. It was not suspended in any great numbers in the water column and either developed during

early summer from a small seed population remaining in the water, or from akinetes and heterocysts resting in the mud.

E. STRATIFICATION OF THE ENTIRE COMMUNITY OF PHYTOPLANKTON

A maximum in total phytoplankton volume during summer developed within the thermocline, or in the upper region of the hypolimnion. Typically, Deming supported a sharply-delineated peak between 4.5 and 5.0 m (Fig. 22). Josephine supported two metalimnetic maxima. Arco had two metalimnetic and one hypolimnetic peak (Fig. 23).

The gradients in volume through the depth column were usually large, often exceeding a six to ten-fold change within a 20 cm depth interval. Thus even with the close intervals, sampling the phytoplankton microstructure had not been satisfactorily resolved and the degree of microstructure recorded was undoubtedly a conservative estimate of the complex heterogeneity which must have been developed both by individual species and by the entire phytoplankton community.

Although greater precision in community distribution could be obtained simply by sampling at closer depth intervals, there may be no justification in expending the time necessary to double the number of algal counts. The main point has been made, that models of lake systems cannot ignore the complexity which has been shown to occur in the distribution of the phytoplankton. Also, because of the microstratification, satisfactory estimates of lake biomass, whether of individual species or of the entire community, cannot be made on the basis of surface samples, integrated samples (since lakes are not cubic in shape), or even

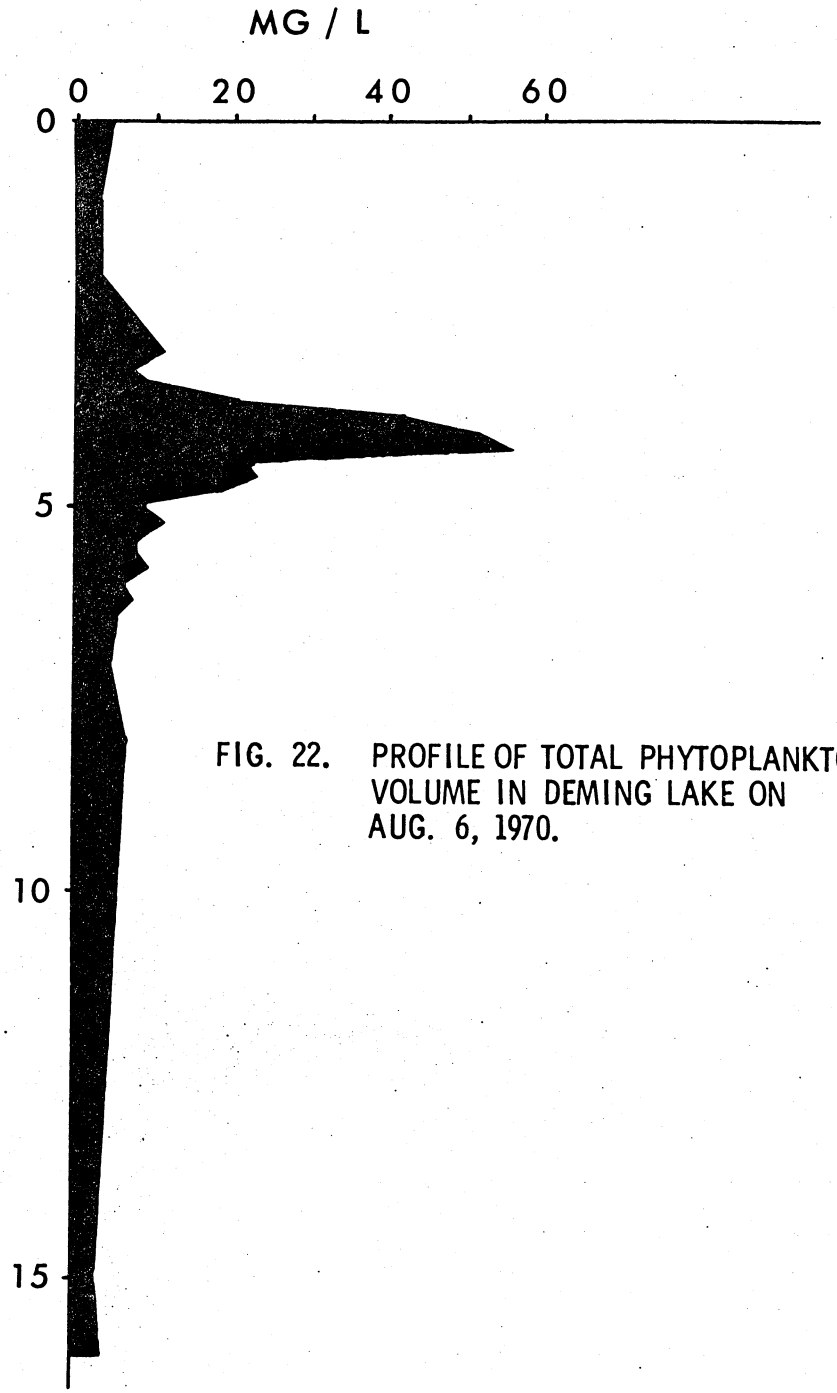
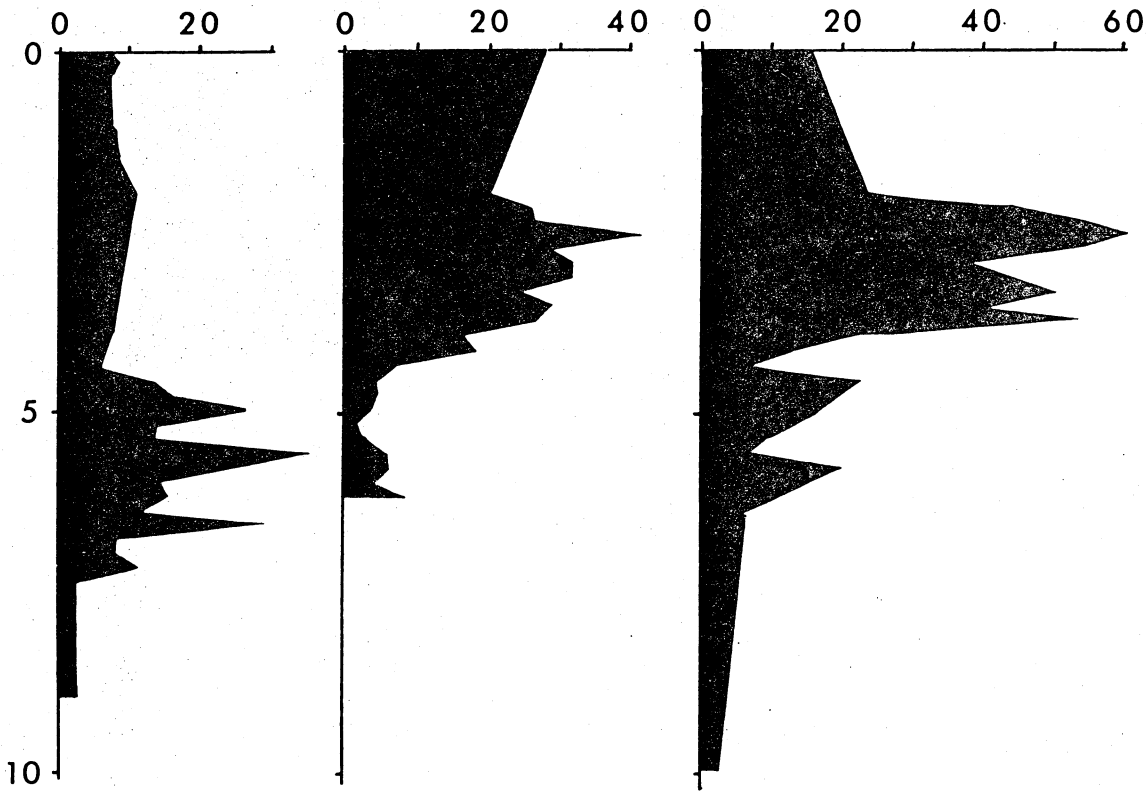


FIG. 22. PROFILE OF TOTAL PHYTOPLANKTON VOLUME IN DEMING LAKE ON AUG. 6, 1970.

FIG. 23. PROFILES OF TOTAL PHYTOPLANKTON VOLUME, EXPRESSED AS THE FRESH-WEIGHT EQUIVALENT (MG/L), ON MAY 25, JUNE 28, AND JULY 9, 1970.



of in-depth samples taken at intervals that may well miss sharply-defined strata and within which may reside the majority of the lake biomass.

F. SIMILARITY OF OPTICAL DENSITY AND TOTAL VOLUME PROFILES

Visual inspection of the profiles of O.D. and total algal volume (standing crop) shows sufficient agreement to at least support the contention that algal stratification is responsible for the observed microstructure within the O.D. profiles (Baker and Brook, 1971). The major peaks and valleys in both volume and O.D. occur at similar or identical depths, and the thickness of the strata is comparable. Peaks in algal volume profiles occasionally were at depths greater than respective peaks of O.D., and tended to be less sharply delineated. These differences may well have been the result of the sampling methods employed. The turbidometer was always lowered through the depth column before other submersible probes, to minimize artificial mixing of the strata. Thus, the difference in disturbance, as well as in the degree of resolution, between the methods of determining O.D. and algal volume may be sufficient to account for the observed profile differences.

Less convincing is the inconsistency in peak size, where more than one peak is present. The three major peaks in O.D. in Arco, for example, are of equivalent magnitude, while the three peaks in algal volume are quite unequal, the shallowest peak being by far the largest.

Overall similarity of the profiles is apparent, but not at the level of the finest microstructure. The steep gradients

in algal concentration made it very difficult to obtain a close replication of volume, as noted above. The remarkable similarity in O.D. profiles even at different stations on succeeding days suggests that the turbidometer provides a more accurate measure of vertical lake microstructure than does the microsampler.

G. SEASONAL SUCCESSION OF DOMINANT SPECIES

The succession of species may be defined as a change in the dominance-ranking of species in a particular community at any time during the year. Dominance, and change of dominance, are the criteria which have been used for the purpose of assessing succession (Woodruff, 1912; Odum, 1959). The shift in rank of only a few of the most dominant species was considered.

The apparent extent of succession is dependent upon the proportion of the data examined from the depth column, as well as the type expression of data. For example, in Deming, it was found that succession appeared to occur when only surface data were considered. However, when samples from all depths were included there was no indication of succession of species in the lake.

As previously mentioned, there are several ways of expressing the abundance in depth of individual species. Also, dominance may be expressed in several ways. For example, dominance may be expressed in numbers or volume, and per unit area at the deepest station, or per unit volume of the entire lake. Data from the surface sample may incorrectly be considered representative of the entire lake; or representative samples from the entire depth column may be included.

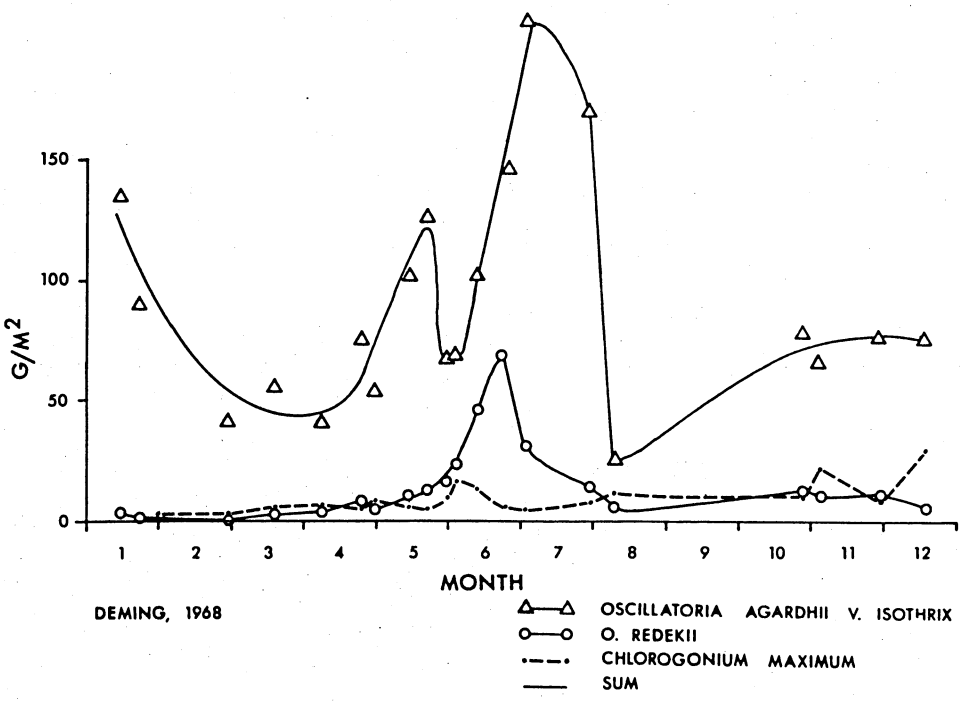
When dominance was expressed as either percent volume, or as the volume of a species present per unit surface area of the lake, and samples from throughout the depth column were taken into consideration, seasonal succession was apparently absent in Deming throughout the year 1968, and nearly absent in 1969 (Figs. 24. 25. 26). Unquestionably, Oscillatoria agardhii v. isothrix was overwhelmingly dominant in the lake.

If dominance was expressed as volume of each species per unit volume of lake water (tons in lake), by weighting the species abundance data by the lake volume at each sample depth, there was only a slight indication of succession in Deming during 1968 (Fig. 27). In contrast, succession of species was found to be of great importance in Deming when the surface sample data were considered to be representative of the entire lake (Figs. 28, 29). This was because the surface "succession" resulted from the descent of several dominant species from the surface waters at the onset of summer stratification. Surface succession during the summer was the result of presence of certain plankters at the surface, such presence in turn being sensitive to small changes in the vertical mixing of the upper two or three meters of the lake.

No species succession appeared to occur during the winter regardless of how the dominance was expressed, as Oscillatoria agardhii v. isothrix was invariably predominant in Deming under the ice.

The relationship between the relative degree of seasonal succession in Deming during 1968, and the type of expression

FIGURE 24. Seasonal variation in the aerial volume of the three most dominant phytoplankton species in Deming Lake, 1968, based on profile samples.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MONTH
DEMING, 1968
OSCILLATORIA AGARDHII V. ISOTHRIX
O. REDEKII
CHLOROGONIUM MAXIMUM
SUM

FIGURE 25. Seasonal variation in the percent volume of the three most dominant phytoplankton species in Deming Lake, 1968, based on profile samples.

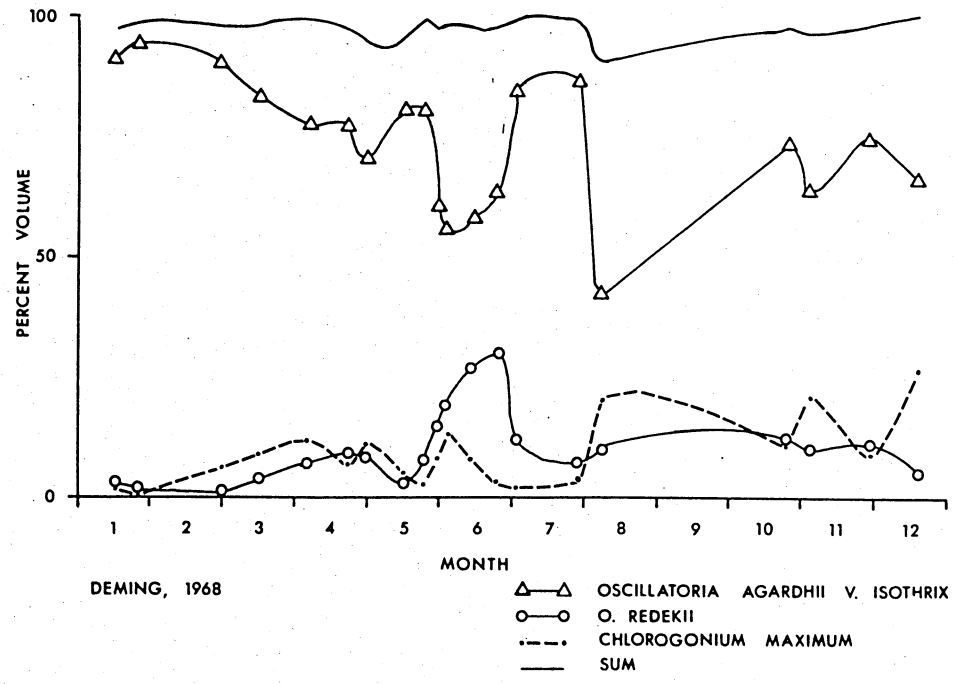

100
50
0
PERCENT VOLUME
1
2
3
4
5
6
7
8
9
10
11
12
MONTH
DEMING, 1968
OSCILLATORIA AGARDHII V. ISOTHRIX
O. REDEKII
CHLOROGONIUM MAXIMUM
SUM

FIGURE 26. Seasonal variation in the percent volume of the three most dominant phytoplankton species in Deming Lake, 1969, based on profile samples.

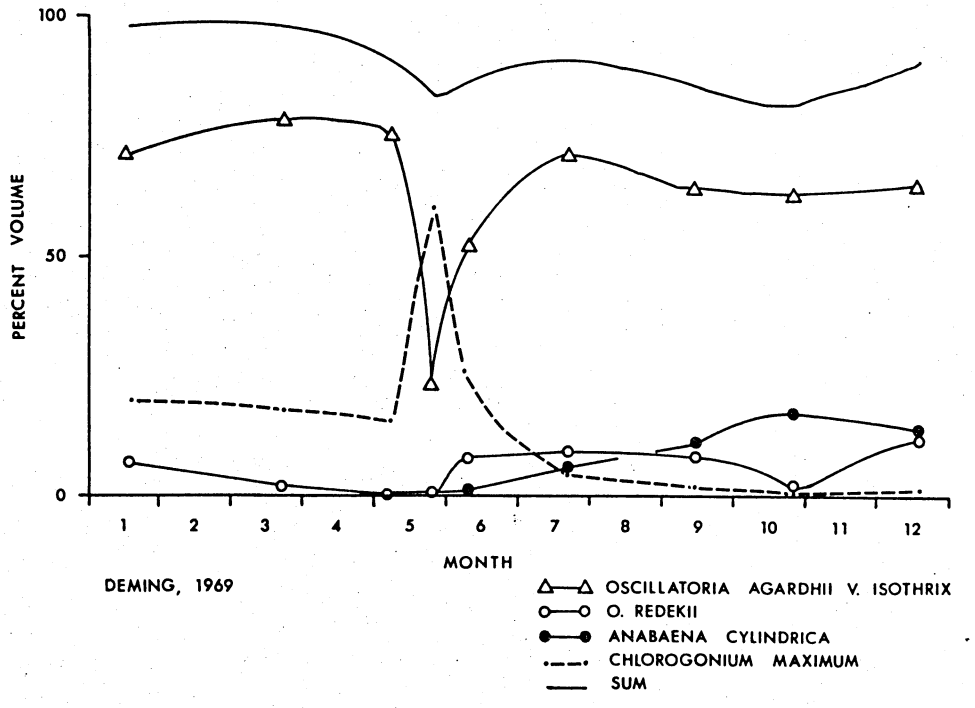

100
50
0
PERCENT VOLUME
1
2
3
4
5
6
7
8
9
10
11
12
MONTH
DEMING, 1969
OSCILLATORIA AGARDHII V. ISOTHRIX
O. REDEKII
ANABAENA CYLINDRICA
CHLOROGONIUM MAXIMUM
SUM

FIGURE 27. Seasonal variation in the total biomass (tons) of the three most dominant phytoplankton species in Deming Lake, 1968, based on profile samples.

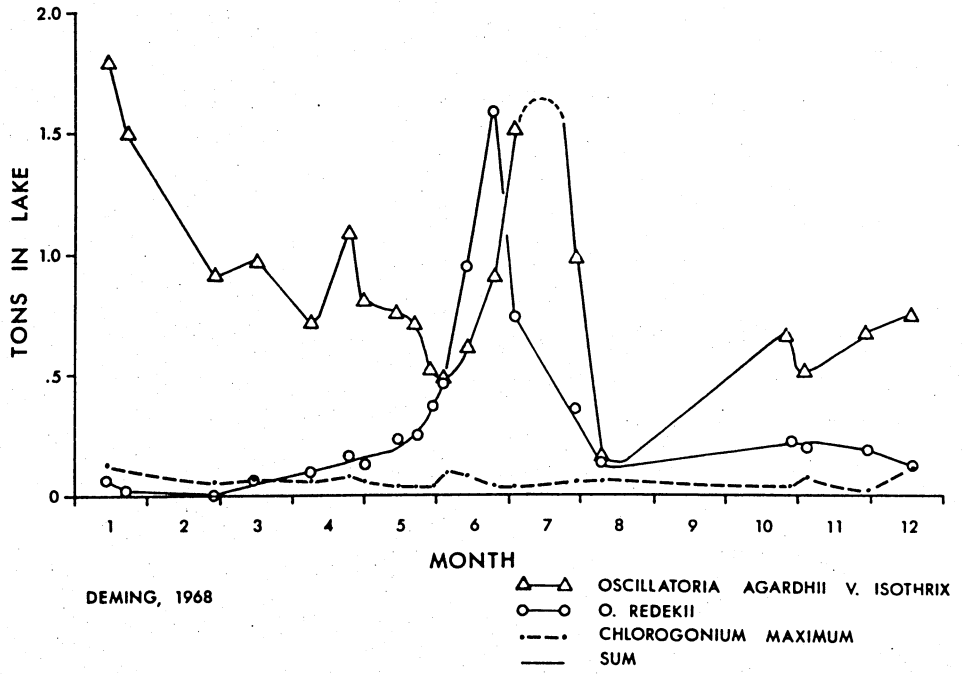

2.0
1.5
1.0
.5
0
TONS IN LAKE
1
2
3
4
5
6
7
8
9
10
11
12
MONTH
DEMING, 1968
OSCILLATORIA AGARDHII V. ISOTHRIX
O. REDEKII
CHLOROGONIUM MAXIMUM
SUM

FIGURE 28. Seasonal variation in the percent total phytoplankton numbers, of the three most dominant species in Deming Lake, 1968, based on surface samples.

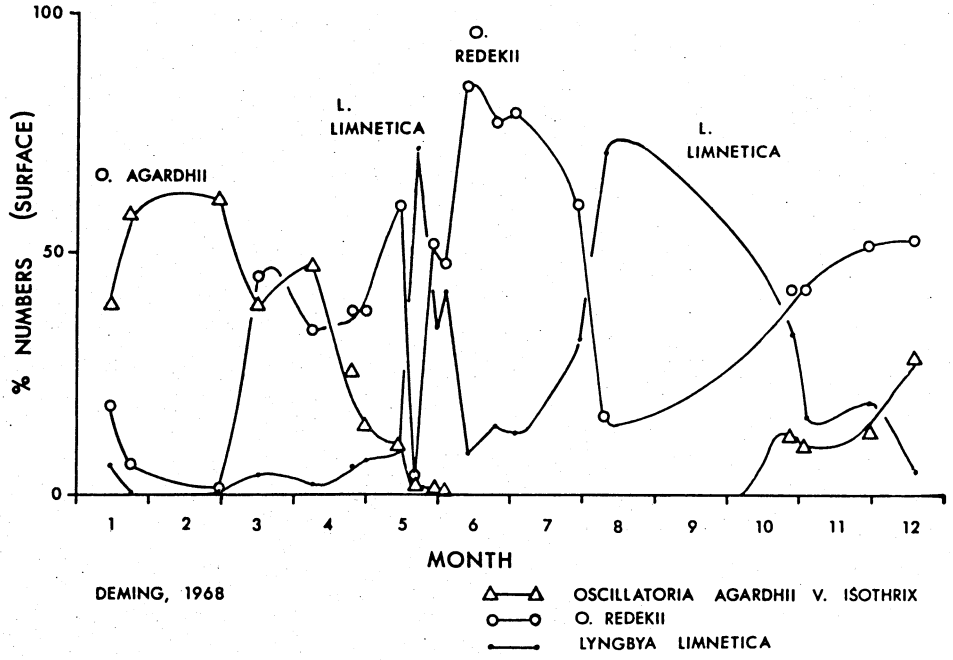
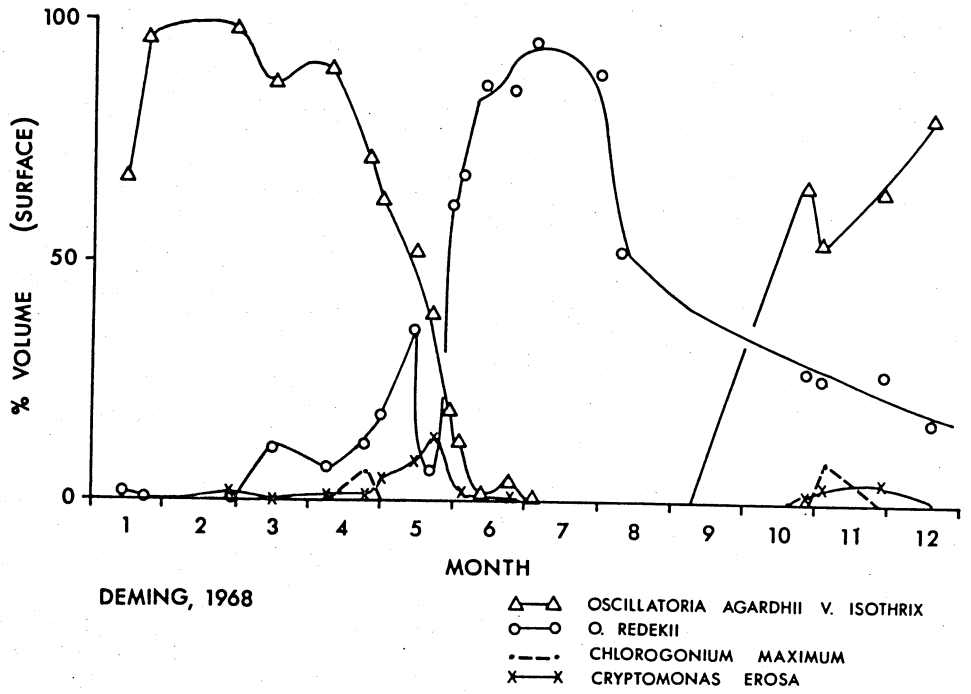

100
50
0
% NUMBERS (SURFACE)
O. AGARDHII
L. LIMNETICA
O. REDEKII
L. LIMNETICA
1
2
3
4
5
6
7
8
9
10
11
12
MONTH
DEMING, 1968
OSCILLATORIA AGARDHII V. ISOTHRIX
O. REDEKII
LYNGBYA LIMNETICA

FIGURE 29. Seasonal variation in percent total phytoplankton volume, of the three most dominant species in Deming Lake, 1968, based on surface samples.


100
50
0
% VOLUME (SURFACE)
1
2
3
4
5
6
7
8
9
10
11
12
MONTH
DEMING, 1968
OSCILLATORIA AGARDHII V. ISOTHRIX
O. REDEKII
CHLOROGONIUM MAXIMUM
CRYPTOMONAS EROSA

of dominance used as a criterion of succession is summarized in Table 2.

Table 2. The relationship between the type of expression of dominance and the relative amount of succession of species in Deming during 1968. (+++ most apparent succession, + least apparent succession, - no apparent succession).

Expression	Numbers	Volume
Surface sample alone	+++	++
Entire depth column, expressed per unit volume of lake water	++	+
Entire depth column, expressed per unit area of lake surface	+	-

A seasonal succession of species was apparent in lakes Josephine and Arco, even when dominance was expressed as volume of species Anabaena cylindrica was important to both lakes, perhaps to the exclusion of Oscillatoria agardhii v. isothrix. During the middle and late summer, A. cylindrica was very abundant, but virtually disappeared from both Josephine and Arco during the winter. Another species becoming dominant for a brief period during late winter was Oscillatoria ornata. The population formed an intense surface bloom under the ice of Arco, but stratified only for a brief time after ice-melt before settling onto the bottom mud. The dinoflagellate Peridinium

cinctum and the cryptophycean Cryptomonas erosa also briefly attained dominance at various times.

In each of the study lakes, seasonal succession was of much less consequence than was the vertical succession of species present during both summer and winter. Three major questions arise from this observation: (1) Can seasonal succession of species be increased in a lake by decreasing the lake's thermal stability? (2) Is such an increase the result of the increase in vertical mixing? (3) Are vertical and seasonal succession mutually exclusive?

H. SEASONAL VARIATION OF BIOMASS

The total biomass (fresh weight) of the phytoplankton in Deming, determined from plankton volume estimates, ranged from 0.3 - 2.8 tons. During the 3-year study period, the biomass varied seasonally in what may be a bimodal pattern (Fig. 30). Maxima occurred both in winter and in early summer each year, and also in late summer, 1969. Minimal biomass values were found during spring and fall mixing.

The early summer maximum occurred 4-8 weeks after ice-melt. An increase during that period of the filamentous blue-greens Oscillatoria redekii and O. agardhii v. isothrix accounted for the biomass peak in 1968. The early summer peak in 1969 was primarily the result of an increase in the green flagellate Chlorogonium maximum, while the two Oscillatoria species increased less rapidly and reached their maximum accumulation a month later. In 1970, the early summer peak was again due primarily to a rapid growth of O. redekii, and also of Anabaena cylindrica,

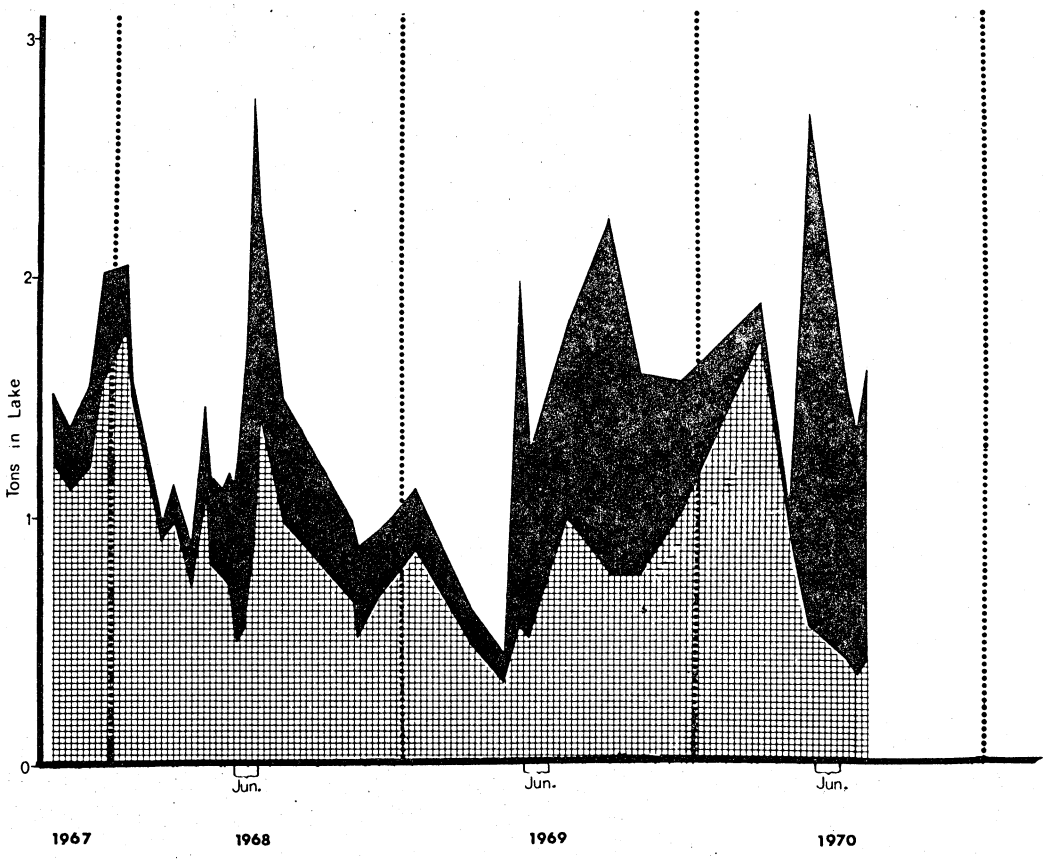


FIG. 30. THREE-YEAR VARIATION (1967 - 1970) IN THE TOTAL PHYTOPLANKTON ABUNDANCE, EXPRESSED AS TONS FRESH-WEIGHT. (CROSS-HATCH: ABUNDANCE OF THE PREDOMINANT SPECIES, OSCILLATORIA AGARDHII V. ISOTHRIX, IN DEMING LAKE. BASED ON PROFILE SAMPLES.

another filamentous blue-green which had in previous years remained sub-dominant.

In contrast to the spring growth in 1968-1969, O. agardhii v. isothrix declined throughout the spring of 1970. The early summer peak in total biomass was consistent, but the development of individual species-biomass varied greatly from year to year.

At all times (other than the falls of 1969-1970) throughout the period October 1967 through August 1970, from 65-98% of the total algal biomass was constituted by the two species O. redekii and O. agardhii, the latter alone accounting for more than 95% in late winter. Anabaena cylindrica never exceeded 6% of the total biomass during 1967-1968, and it decreased to less than 1% each winter.

During the summer and fall of 1969 A. cylindrica developed a dense stratum between those of O. redekii and O. agardhii v. isothrix, and amounted to 24% of the biomass by October, 1969. Again in 1970, A. cylindrica became dominant, already having reached 28% of the total phytoplankton biomass by the time the study ended in August. It is of interest that O. agardhii v. isothrix did not develop dense strata in 1969 and 1970, when A. cylindrica was accumulating. The difference in biomass of O. agardhii v. isothrix between late summer, 1968, and that of 1969 and 1970, is almost exactly compensated for by the increase in biomass of A. cylindrica. The shift in dominance from one species to another may have been directly related to an artificial modification of the lake chemistry by experiments carried out during 1969-1970 on Deming. The experiments involved the pumping of nutrient-rich

metalimnetic and hypolimnetic water to the surface. Because of the small size of Deming, the pumping may well have stimulated the growth of A. cylindrica. It is suggested that the concurrent decrease in the growth of O. agardhii v. isothrix in the enriched water was due to shading of sunlight by the development of the shallower stratum of A. cylindrica rather than by the possible surface enrichment.

Seasonal changes in the total biomass, and in that of individual species in Deming, were also computed on the basis of algal concentrations at the surface of the lake. As before, a biomodal annual curve results, but the peaks and valleys are exaggerated relative to those plotted with data from the entire water column (Fig. 31). Oscillatoria agardhii v. isothrix appeared with surface-water analysis to be a winter form, disappearing entirely from the surface in summer. Quite contrary to results obtained with surface data, an analysis of data from throughout the depth profile has shown that this predominant species continually declined in biomass during fall mixing, and increased at the time of the early-summer maximum.

The total biomass in Arco from June 1969 through July 1970 ranged from 0.2 to 3.0 tons, and is comparable to that found in Deming, although the former lake has only 1/3 the water volume of Deming (6 Ha -m, compared to 17.5 Ha -m). No winter peak in biomass occurred in Arco, but both an early and a late summer peak developed during 1970. The early summer peak was comprised of Peridinium cinctum (56%), a perennial dinoflagellate, and of Oscillatoria ornata (34%), a filamentous blue-green present only

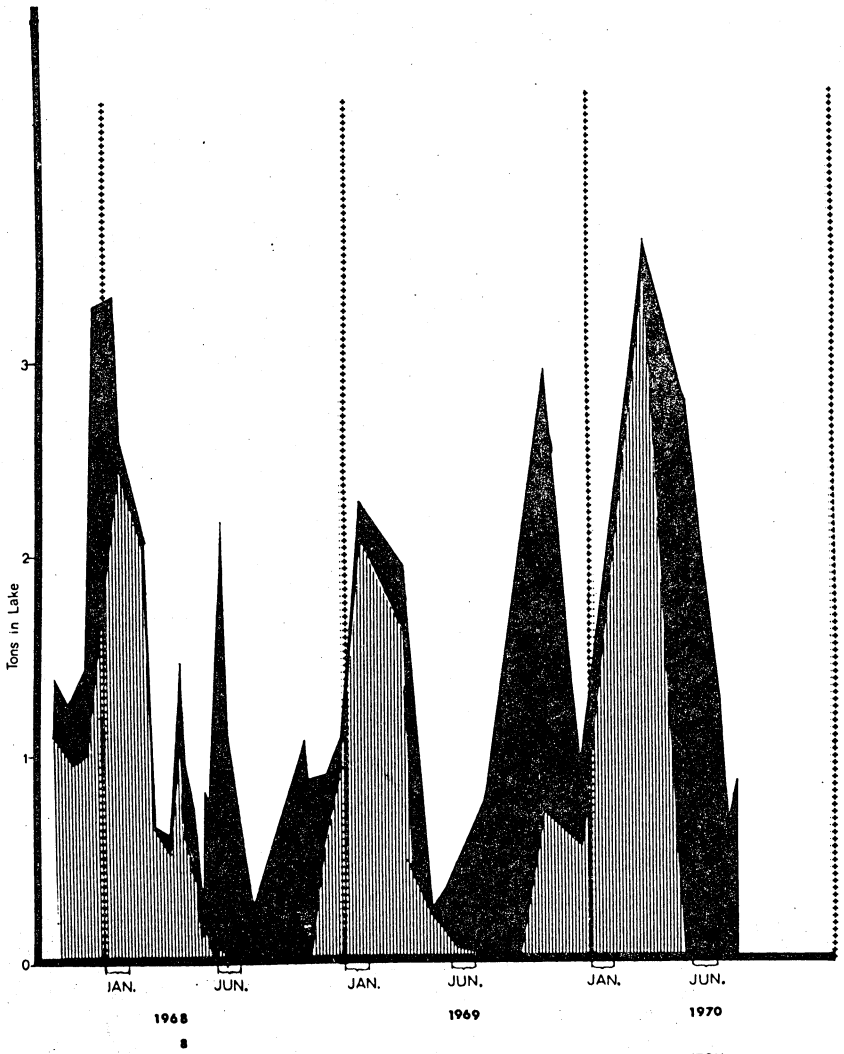


FIG. 31. THREE-YEAR VARIATION (1967 - 1970) IN THE TOTAL PHYTOPLANKTON ABUNDANCE, EXPRESSED AS TONS FRESH-WEIGHT. (CROSS-HATCH: ABUNDANCE OF THE PREDOMINANT SPECIES, OSCILLATORIA AGARDHII V. ISOTHRIX, IN DEMING LAKE. BASED ON SURFACE SAMPLES.

in late winter-early spring. The colonial blue-green Thiopedia rosea formed a very dense hypolimnetic stratum during summer, and a relatively sparse winter stratum under the ice. However, because of its small unit volume (57 cu. micra) and the small volume of water it occupies during summer (less than 5%), this species has little influence on the total phytoplankton biomass value.

For lack of bathymetric data, the volume of lakewater in Josephine, and consequently the total standing-crop, could not be calculated.

I. PRODUCTIVITY PROFILES

The profiles of productivity during summer stratification resembled Findenegg's (1963) type III lake profiles, in having a relatively low surface value and a metalimnetic maximum in oxygen production. The maximum concentration of algae occurred at depths beneath that of the photosynthetic maximum, at light levels of much less than $0.1\%I_0$. The euphotic zone extended to the base of the chlorophyll maximum, which was estimated by relative color development on white membrane filters. Where double peaks in chlorophyll occurred a double peak in productivity was also observed. All algal strata were within the euphotic zone. Productivity of the pigmented bacterium Thiopedia rosea was not measurable by the oxygen technique, and its stratum was in anoxic water.

Winter profiles had a maximum at or near the surface, with the euphotic zone reduced to the upper 3m of the lake. Surface photoinhibition occurred only on clear days.

J. DIVERSITY PROFILES

Diversity index profiles (Shannon-Weaver index) during summer stratification tend to be minimal both near the surface and in the hypolimnion, and maximal in the metalimnion. Diversity values of successive samples separated by 20 cm in the depth column tended to fluctuate over a wide range (0.5 to 3.0) within the thermocline. The lowest values were always associated with a dense, relatively isolated algal stratum. The highest values resulted from an overlap of several strata of similar density. It became clear that any further interpretation of the relative diversity values of the neighboring samples would be meaningless.

The low values near the surface and in the upper hypolimnion were associated with a single predominant population, usually of low and high cell concentration respectively.

The winter diversity profiles tended to be maximum near the surface, in association with the production maximum.

K. LABORATORY COLUMN EXPERIMENTS

Laboratory column experiments designed to show the relative importance of light intensity and temperature on vertical migration of Deming Lake phytoplankton clearly demonstrated that buoyancy regulation is driven by light and is only secondarily (if at all) dependent upon temperature in the range of 3° to 15° C.

The first experiment with two laboratory columns demonstrated that reversals in migration occur at a time scale of a few days in response to switching from light to dark or dark to light, in a 3°C isothermal column. Three sequential reversals were observed

in one column, two in the second column (Table 3). In all except the final incubation of column 1, migration was downward in the light and upward in the dark.

The predominant alga was Oscillatoria agardhii v. isothrix, as in the metalimnion of Deming Lake. The species formed a dense surface bloom within one day of dark incubation, and was absent from the surface within one day of light incubation. The filaments appeared healthy during the first six weeks of incubation, but deteriorated during the last two weeks. At the end of the experiment, the majority of filaments had formed "clumps" and appeared partially chlorotic. The "clumps" at the bottom of the columns were the most deteriorated.

The second experiment with four laboratory columns demonstrated that O. agardhii v. isothrix, as well as several less-abundant phytoplankters (O. redekii, Cryptomonas erosa, Synedra acus, Dinobryon sertularia) will migrate downward or upward in response to light and dark incubation respectively, through a very steep thermocline (2.7°C/10cm). (Table 4). No reversals were carried out. However, the optical density profiles were very stable in all four columns.

In the isothermal columns, strata were not well defined at intermediate depths. The response to light or dark incubation was to migrate to the bottom (2.0m) or surface respectively. Near the end of the four-week incubation period, a slight optical density maximum developed at 0.8m (Table 4). Nevertheless, the apparent trend in this column was a sedimentation onto the bottom.

TABLE 3. LABORATORY COLUMN EXPERIMENT #1.

TIME	COLUMN #1	COLUMN #2
0 DAYS	MIXED	MIXED
+7 DAYS	DARK ↑	DARK ↑
+2 DAYS	LIGHT ↓	DARK ↑
+13 DAYS	DARK ↑	LIGHT ↓
+17 DAYS	DARK ↑	LIGHT ↓
+6 DAYS	LIGHT ↓	DARK ↑
+13 DAYS	LIGHT (↑)	DARK ↑

(TOTAL 58 DAYS)

(ARROWS: Direction of algal migration, based on O.D. changes)

TABLE 4. LABORATORY COLUMN EXPERIMENT #2.

DEPTH OF MAXIMUM OPTICAL DENSITY

TIME	COLUMN #1 (LIGHT, 15°+ THERMOCLINE)	COLUMN #2 (DARK, 15°+ THERMOCLINE)	COLUMN #3 (LIGHT, 3° THERMOCLINE)	COLUMN #4 (DARK, 3° ISOTHERMAL)
0 DAYS	MIXED	MIXED	MIXED	MIXED
14 DAYS	0.4m	SURFACE	BOTTOM	SURFACE
28 DAYS	0.4m	SURFACE	(0.8m)	SURFACE

In contrast, a well-defined maximum optical density developed at 0.4m within a few days in the illuminated column having a thermocline between 0.3 and 1.5 m. A secondary peak was also present at 0.8m. Analysis of the samples showed that Oscillatoria redekii and Synedra acus were co-dominants near the 0.4m maximum, along with Dinobryon sertularia. The lower peak was comprised almost entirely of O. agardhii v. isothrix and Cryptomonas erosa. The "ordination" of the several dominants similar to that in the study lakes developed in this column. The re-ordering of species in the columns seemed especially remarkable, as the lake sample had been collected from the metalimnion of Deming Lake (5m) in mid-June. At that time, the algal strata in the lake were well established. The sample from 5m must have collected epilimnetic species that had descended from their original strata. They re-established themselves as epilimnetic populations within the laboratory columns. A plausible interpretation is that the 5m lake sample was relatively "enriched" with dissolved nutrients, and that algal growth in shallower lake strata were already limited by these nutrients. The resuspension in the laboratory columns of the epilimnetic forms with the "enriched" metalimnetic water may have been sufficient to rejuvenate their buoyancy-regulating mechanism.

DISCUSSION

The primary objectives of this study have been to critically examine and describe the distributional relationships between members of the phytoplanktonic community of three small lakes.

Distributional patterns of abundance, rather than simple presence-absence, have been quantified during the three-year study period.

A distributional pattern of considerable complexity was observed throughout the study and during all seasons. It is clear that characterization of lake phytoplankton may require careful and extensive sampling throughout the depth column and throughout the year, especially if ecological relationships of species and environmental factors are to be determined. One-shot surface samples are outmoded and completely unsatisfactory. Most of the species found are in the nannoplankton range (< 25 μ diameter), so that plankton net samples would have been unsatisfactory.

It may be suggested that the results of this study apply only to the rather extreme lake type selected: All of the study lakes are thermally stable with a very shallow (less than 6m) thermocline, and with the euphotic zone protruding into the hypolimnion. However, the position is taken here that all lakes support stratified layers of phytoplankton. The degree of stratification was found to be related to the thermal (or chemical) stability of the lake. The present study has demonstrated that taxonomic affinity (of species) tends to have little relation to their vertical distribution. The epilimnetic species thrive in high temperature, high light intensity, and low nutrient concentration. The hypolimnetic species develop in very low light intensity, low temperature, but in high concentrations of dissolved nutrients. The metalimnetic group, perhaps the most interesting, is comprised of many species each of which may stratify independently within

a microenvironment and along a nearly continuous gradient of very different habitats.

Mechanisms which have been proposed to account for the formation of algal strata fall into three general categories and include 1) phototaxis, 2) regulation of buoyancy, and 3) minimum turbulence in the depth column.

Phototaxis is an active movement of an organism toward (positive) or away from (negative) a light source. Among the phytoplankters, flagellated forms have the most obvious mechanism for active movement, and Chlamydomonas spp. as well as Euglena spp. have long been known to migrate in response both to light intensity and wave length.

Regulation of buoyancy may be achieved by a differential uptake of dissolved substances, by a differential production of light-weight storage products, by differential production accumulation of extracellular mucilage, and (only Cyanophyceae) by control of relative gas vacuole volume to total cell volume (Fogg, 1965).

The only evidence for selective uptake of monovalent ions is by the marine diatom Ditylum brightwelli, which renders the cells slightly less dense than in the absence of the ion selection. Although Fogg points out that in freshwater such ion selection would never decrease the density of a diatom to less than that of the water, it is still true that any reduction in cell density will slow its rate of descent in a water column of given density. (Stoke's Law includes the factor p-p', the difference between the density of water and that of a suspended particle. For a

discussion, see Hutchinson, 1967. Further, it is readily observable that the settling rate of preserved algal cells (as in a sedimentation chamber) is a function of the type preservative used. Of the addition of iodine, methyl-mercury, and formalin, iodine causes the most rapid settling rate and formalin the least (sometimes even a negative rate). This artificial manipulation of cell density may be evidence of an analogous phenomenon in living cells.

A change in cell density as a function of the population growth phase has been observed by Fogg (1965) in cultures of Botryococcus braunii, as a function of the reproductive cycle by Tamiya (1963) in cultures of Chlorella ellipsoidea, and as a function of low light intensity by Steele and Yentsch (1960) in the marine diatom Skeletonema costatum.

The effectiveness of gas vacuoles to modify the density of blue-green cells has been reviewed by Walsby (1972). He has grouped the various hypotheses into 1) differential production of gas vacuoles, and 2) collapse of gas vacuoles. Walsby described the gas vacuole as being a repository for whatever gas happens to be available, and as such a floatation device. The higher the relative gas vacuole volume to total cell volume, the lower the cell density. Evidence from algal cultures (Smith and Peat, 1967; Lehmann and Jost, 1971) has demonstrated that gas vacuolization is low in rapidly-growing cells, and high in older slowly-growing cells of Anabaena flos-aquae, Microcystis aeruginosa, and Oscillatoria redekii. Further, these same phytoplankters tend to have low gas vacuolization in high light

conditions. During the present study, gradations within a stratified population of O. redekii were repeatedly found from relatively low gas vacuolization (almost none visible in the inverted microscope) in the upper layers of the stratum, to high vacuolization in the lower layers. A similar but much less obvious relationship was seen in the stratum of O. agardhii v. isothrix. Occasionally segments of individual filaments showed differing degrees of vacuolization. Lehmann and Jost's suggestion of gas vacuole dilution by rapid cell growth would seem appropriate to explain such observations.

Walsby proposed a second mechanism to reduce buoyancy by modification of the degree of gas vacuolization, the collapse (and destruction) of the gas vacuoles by an increase of cell turgor pressure as the result of a build-up of photosynthate during periods of high photosynthetic activity. Evidence was not observed in the present study to add to Walsby's hypothesis; the degree of gas vacuolization in migrating populations of O. agardhii v. isothrix in light and dark laboratory columns should have been observed.

Pfennig and Cohen-Bazire (1967) suggested that the formation of gas vacuoles in photosynthetic bacteria occurs only at low temperatures (4-8°C).

Hill (1966) observed a very rapid vertical migration by Aphanizomenon flos-aquae as a response to alternating periods of light and dark. The rafted filaments, previously collected from the surface of a small pond, migrated within minutes to the bottom of a quart jar when placed in a darkened refrigerator. When again

exposed to bright sunlight, the "rafts" equally rapidly floated to the water surface inside the jar. Neither vavuole collapse nor vacuole dilution by cell growth is an adequate explanation of such a rapid response to light and dark reversals. However, the collective effect of many filaments attached in a single raft with a large radius may explain the rapidity of migration (which is a function of γ^2 in Stoke's Law).

Algal strata have been reported to occur primarily in small, physically stable lakes. However, strata have developed in even the least stable polymictic lakes in Africa (see Introduction). Moreover, close-interval or continuous column sampling across thermal gradients has shown complex layering to be present even in the ocean (Strickland 1968).

The above hypotheses and observations suggest that buoyancy is regulated in part by light, and possibly by temperature. Zimmerman (1969), while not mentioning the relative amount of gas vacuolization, observed that Oscillatoria rubescens descended during early summer from 7.5 to 12.5 m following the 1.9 ppb phosphorus isopleth and leaving in its wake a depressed phosphorus concentration of 0.6 ppb. When phosphorus increased later in the summer to 1.9 ppb at 5m, O. rubescens again formed a stratum at that depth. This is clear evidence that buoyancy may be regulated as a response to nutrient concentration. In this case, the formation of gas vacuoles was dependent upon a sufficient phosphorus concentration.

Other workers have observed a succession from blue-greens to greens upon addition of phosphorus to lake columns (Thomas

1964, Klemer 1973). A review of possible nutrient relationships and buoyancy regulation has been prepared by Klemer (Ibid.) that emphasizes the importance of ammonia in the formation of (cyanophycean) gas-vacuoles.

Brock (1973) has emphasized that blue-greens rarely tolerate low pH (<4.5) and are usually abundant only at high pH (>@ 8.). Shapiro (1973) has observed in "bag" experiments that blue-greens are favored at high pH levels, and are replaced by greens at lower pH values even when enriched with nitrogen and phosphorus. In the present study, high pH values (from 8.5 to 11.3) were invariably associated with the blue-green strata. Low pH levels (6.2 to 6.5) were always present in the hypolimnion immediately beneath the pH maxima. A possible advantage of stratum formation is pH modification by the blue-green populations.

Minimum turbulence, which occurs in regions of maximum temperature gradients, was invoked by Lund et al. (1963) to explain a maximum abundance of Asterionella formosa Hass in Lake Windermere. In such situations, the sedimentation rate of the cells is relatively unaffected. Cells in the epilimnion are passively swept by turbulence up and down through the region. Once reaching the thermocline the cells may accumulate but are transient, and are again swept by turbulence once having descended beneath the thermocline. An analogous distribution of suspended particles was observed in the upper atmosphere (Goldberg and Aiken, 1973). Metallic ions of extraterrestrial origin were found to be settling during a meteor shower. An accumulation or maximum abundance of the ions (as much as ten-fold) in a narrow

stratum (2.5 km thick, at 112 km above ground) coincided with a shear zone between two turbulent air masses. The shear zone was apparently a region of minimal turbulence.

Were such a passive role played by the descending algal cells, a single profile shape should result -- with all species conforming to the peaks and valleys of the entire community. The observed independent stratification of many species is sufficient evidence to discount this hypothesis.

Further evidence discrediting passive sedimentation comes from sedimentation-trap studies, in which it was found that cells do not sediment into traps placed at depths above their zone of stratification. At the same time, the same cells do settle downward into traps placed beneath the population layer, even as the concentration of cells within the layer increases. The conclusion follows that the cells must be growing and reproducing within the zone of stratification, and are not imported by sedimentation from shallower depths. (Recruitment of cells laterally from the edges of the lakes is an untested but highly unlikely alternative, as O.D. measurements suggested a uniform cell concentration across the lake at each depth.)

Observations with laboratory columns further showed the importance of light in inducing buoyancy changes, especially on Oscillatoria agardhii v. isothrix. Incubation in darkness, whether at low (3°C) or intermediate (15°C) temperature, caused the population to rise to the surface of the column. Illumination (300-500 ft. c) following dark incubation induced sinking, and subsequent dark incubation again caused the population to rise

to the surface. During short-term periods, then, light as a driving force overrides temperature, at least over the range of 3° to 15°C. In these studies, nutrients were not monitored. Independent of any changes in dissolved nutrients the Oscillatoria filaments continued to migrate in response to the series of light-dark reversals.

During the longer period of several summer months, the stratum of Oscillatoria agardhii v. isothrix followed the zone of 1% surface illumination. With an increase in biomass of several other shallower strata and the consequent increase in light extinction during the summer months, the 1% light zone and the O. agardhii v. isothrix stratum moved upward from 6 to 4.5 m. The upward migration of the population was into the warmer water of the thermocline, so that an increase in its buoyancy must have been necessary.

Whatever the environmental factor was that drove the stratification observed during the present study, both buoyancy regulation and phototaxis were probably involved in the formation of the discrete layers of phytoplankton. Minimal turbulence was associated with the majority of the strata. Thus, the thermal microstructure was also important, perhaps as a prerequisite to algal stratification. As previously noted, the only diatoms present were of a most delicate type with extremely fragile frustules (Synedra acus v. angustissima, Rhizosolenia eriensis). "Heavy" forms were conspicuously missing from the plankton of the lakes, although they were common in nearby larger lakes of

greater turbulence (Staurastrum arctiscon, Cosmarium granulosa, and many other desmids, diatoms, and chlorococcalean species).

The flagellated species have a more obvious means of maintaining a position of preference in the depth column, and of migrating when it is advantageous to do so. Even such motile species could conserve energy by regulating their buoyancy to match that of the water surrounding them.

The non-flagellated chlorophycean species which formed layers had no obvious buoyancy mechanism. Chlorococcalean species have been shown to modify their specific gravity by shifting metabolite production in response to light intensity changes (Tamiya 1963).

The importance of light intensity in changing algal density is thus well supported by laboratory and field studies. Light responses alone are not sufficient, however. Formation and persistence of strata also require that the vertical mixing of water in the depth column be sufficiently low that algal cells are not physically swept out of their stratum. The microstructure in the thermal profile of the study lakes was similar in pattern to that of the several algal strata. There was an apparent association of some or all of the algal strata with regions of of greatest temperature gradient (up to 2.2°C/m, over short depth intervals). Alternatively, it is possible that the algal layers were responsible for the development of the thermal microstructure, by absorption and radiation of heat energy from sunlight. In such a way the populations could have modified

their microenvironment thereby enhancing the stability of their position in the depth column.

It was found that the rate of increase of some of the strata varied through the summer. For example, Oscillatoria redekii grew rapidly in early summer, followed by O. agardhii v. isothrix, and later by Anabaena cylindrica. By the time of fall overturn, many species had reduced their growth rate, while maintaining their position within a stratum. The large accumulation of dissolved oxygen and the development of a pH as high as 11.0 within the O. agardhii v. isothrix stratum suggests that growth conditions deteriorated, but not sufficiently to entirely disrupt the stratum. Some of the most concentrated strata apparently reached a steady state between production and sedimentation, with a plateau in concentration (cells/ml). Others declined in concentration. Had summer stratification been prolonged, many of the populations probably would have migrated to greater depths with higher nutrient supplies. Survival (or at least concentration) within the deeper stratum would then depend upon sufficient light intensity. A progressively lower daily light-energy input in late summer-early fall might eventually disrupt the strata, even in the absence of the fall overturn.

Because the thermal, optical, and chemical regimes of the study lakes tend to be stable for prolonged periods during the summer, an ideal situation exists to carry out microenvironmental studies in the separate population layers. During the present study, only temperature was measured with a precision approaching that necessary for such an objective. Non-linear gradients of

light, orthophosphate, pH, conductivity, ammonia, oxygen, CO_2 and HCO_3, Mg, and Fe are known to traverse the plankton layers. It would seem likely that much autecological information might be forthcoming from in situ kinetic studies at depths where the layers persist. The results would certainly enrich some of the alternative hypotheses about the layering, and could possibly explain the more general problem of distribution of species in lake "types" (oligotrophic to eutrophic). Further, studies of atypical mixing in such lakes may provide an answer to the question of an interaction between physical stability and species succession in an aquatic system.

SUMMARY

A three-year study of the planktonic community of three study lakes has been carried out. Among the more important relationships determined are the following:

1. The majority of phytoplankton species tend to stratify, and are prevented from doing so only by vertical mixing of the water column. Strata may develop and persist within narrow (less than 40 cm) depth intervals.

2. The shape of the profile of abundance (units/ml) is species specific. Of the several dominant species, all of the profiles were unique. The profile of a given species tended to be similar in shape (if not in absolute depth) on a given date in different lakes and in separate years.

3. Phytoplankton populations may be grouped on the criterion of the location of their peak abundance into epilimnetic, metalimnetic, or hypolimnetic types.

4. The majority of species in the study lakes form "perennial populations", in the sense that they are present in large numbers throughout the year. (Individual algae were certainly not perennial.) Other populations were ephemeral, and occur briefly during the year either at ice-melt or in late summer.

5. The location of individual strata within the depth profiles is determined at least in part by light intensity. Vertical migration can be induced by modifying the light intensity entering the lake.

6. Micro-gradients in temperature (within a 10 cm depth interval) are usually associated with, and are apparently necessary for, the formation of the most pronounced phytoplankton strata.

7. Peaks in optical density profiles are related to peaks in phytoplankton concentration. The O.D. profiles are similar at stations near shore to those near the center of the small study lakes. For that reason, it is suggested that stratification of phytoplankton is relatively unaffected by nearness to shore. The station at the deepest column may be representative of the entire lake, given a small and simple basin.

8. The initial formation of the metalimnetic and hypolimnetic strata following ice-melt is accompanied by a downward migration or "sedimentation" of phytoplankton.

9. The development and maintenance of high concentrations of individual populations is by cell growth within the population stratum, and is not accompanied by continuous "passive sedimentation" into the layer from shallower depths. However, a continuous "plankton rain" falls out of the stratum.

10. Some or most species of phytoplankton together form a series of strata with a definite spatial arrangement or "ordination" within the depth column. Some species are always located at shallow depths, others at slightly greater depths, throughout the euphotic zone (to a light intensity of less than 0.1% I_0).

11. Metalimnetic and hypolimnetic strata of individual species do not locate at the same absolute depth throughout the summer, but instead tend to migrate slowly upward as light extinction within the column increases. A build-up of shallow layers during the summer is responsible for increased light extinction.

12. A given species locates at different depths, different temperatures, and different light levels and in different basins during any particular time period in the summer. Although both temperature (perhaps temperature gradient) and light may be important causal factors, neither alone is sufficient to explain the observed variations in location of strata. Gradients of dissolved phosphate and ammonia, as well as pH, were observed in the metalimnion. The limited data allow little speculation concerning the interaction of nutrients with temperature and light. The upward migration of metalimnetic strata in

response to decreasing light intensity requires the populations to move into regions of lower phosphate and ammonia concentration. By inference light becomes limiting to growth of the migrating species, and it is therefore responsible for the migration, rather than the dissolved nutrients.

13. Diversity profiles (Shannon-Weaver Index) tend to have a maximum value at intermediate depths. A low diversity value at both the surface and the base of the euphotic zone is associated with extreme environmental conditions, especially light intensity, temperature, pH, and concentration of dissolved substances. The low diversity at the surface is often associated with a low concentration of biomass of phytoplankton, while at the base of the euphotic zone (at least in Arco L. and Josephine L.) with a high concentration of a single species, Merismopedia trolleri (Thiopedia sp. ?).

14. Productivity analysis of the study lakes showed a maximum photosynthetic rate in the metalimnion where a build-up of dissolved oxygen creates a positive-heterograde curve. Photosynthesis was measurable with the oxygen technique to the lower limit of oxygenated water. Only the Merismopedia trolleri population failed to respond in suspended bottles. No dissolved oxygen was measurable in association with the M. trolleri population and if it was producing oxygen, insufficient oxygen was accumulated during incubation to be measurable.

15. Measurement of primary productivity using the technique of suspending B.O.D. bottles at half-meter intervals becomes increasingly inaccurate as phytoplankton stratification increases.

Both the measurement and modelling of phytoplankton growth require special thin-layer sampling techniques when such stratification is encountered.

16. Little seasonal succession of species was observed in the study lakes. It is postulated that the stability of the columns in these particular lakes may be directly responsible for the lack of seasonal succession. A disruption of the columns would eliminate the unique habitats present in thin-layer sections of the stratified columns. The temperature level would fluctuate to a greater extent, deeper in the column. In particular, when the entire euphotic zone becomes mixed, the important thermal gradients disappear and thus the algal strata. All phytoplankton species would be mixed together, and would come into direct competition for nutrients. It is likely that direct competition is a driving force of seasonal succession. Species which are somewhat isolated in layers of a stratified column would experience a minimum of competition.

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APPENDIX I. OPTICAL DENSITY PROFILES IN DEMING, ARCO, AND JOSEPHINE (1968-1971)

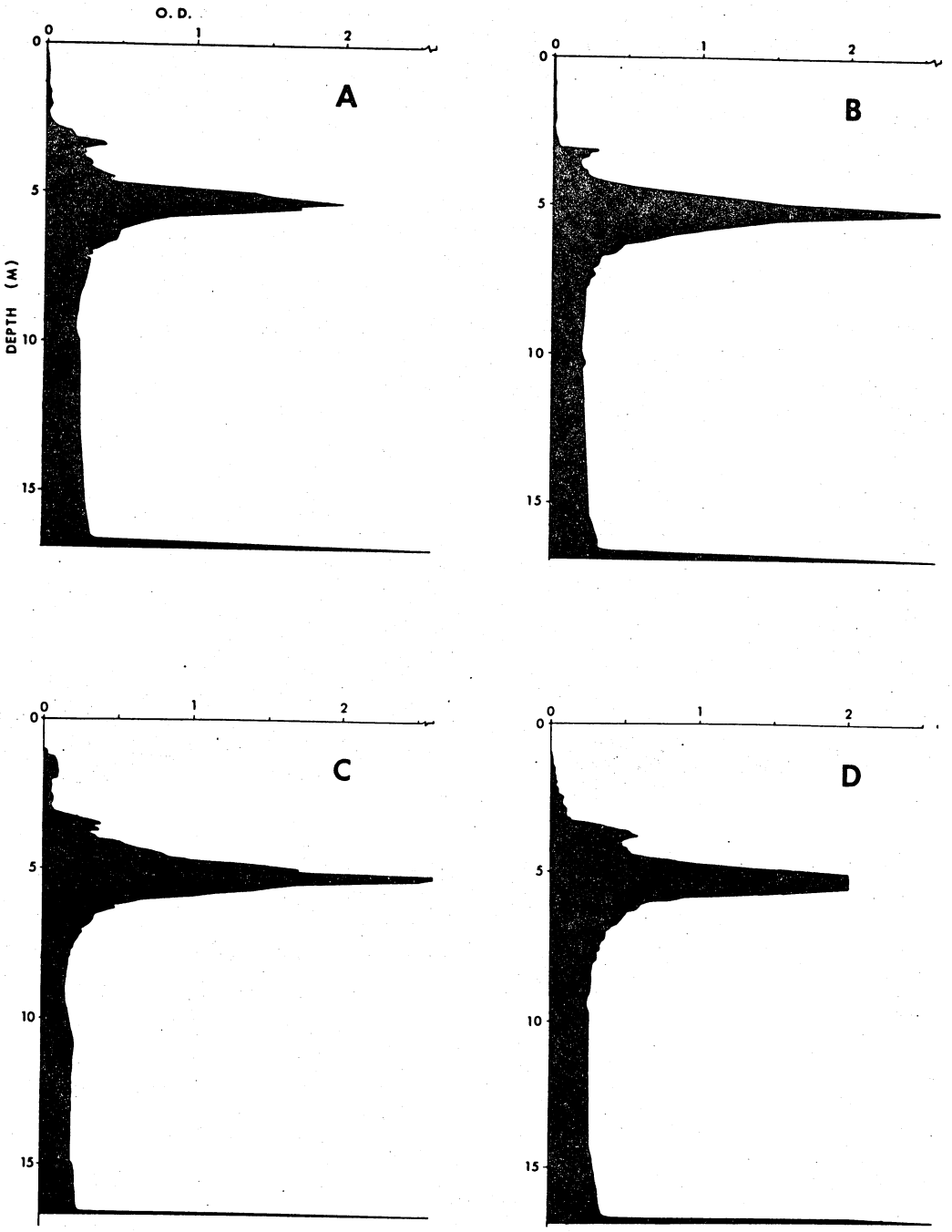
The following optical density profiles are arranged chronologically for each of the three lakes. A key with calendar-dates is located at the beginning of each set of figures.

Each profile is semi-continuous, recorded during the descent of the transmissometer. The optical density was recorded whenever a change was noted, at intervals as close as 5 cm.

Occasionally (e.g. D, E) the peak in optical density appears to be truncated, probably an artifact. The sensitivity of the meter decreases rapidly at O.D. readings approaching 2.000.

DEMING LAKE OPTICAL DENSITY PROFILES

A	June 28, 1968
B	July 1, 1968
C	July 4, 1968
D	July 10, 1968
E	July 11, 1968
F	July 22, 1968
G	July 28, 1968
H	August 2, 1968
I	August 18, 1968
J	September 9, 1968
K	October 27, 1968
L	November 2, 1968
M	November 29, 1968
N	December 18, 1968
O	January 18, 1969
P	May 3, 1969
Q	May 14, 1969
R	May 24, 1969
S	June 9, 1969
T	July 21, 1969
U	August 2, 1969
V	August 15, 1969
W	September 14, 1969
X	October 25, 1969
Y	March 21, 1970
Z	May 3, 1970
AA	May 24, 1970
BB	June 14, 1970
CC	June 27, 1970
DD	July 10, 1970
EE	August 6, 1970
FF	August 16, 1970
GG	October 17, 1970
HH	April 11, 1971
II	May 11, 1971
JJ	June 7, 1971
KK	July 20, 1971
LL	August 9, 1971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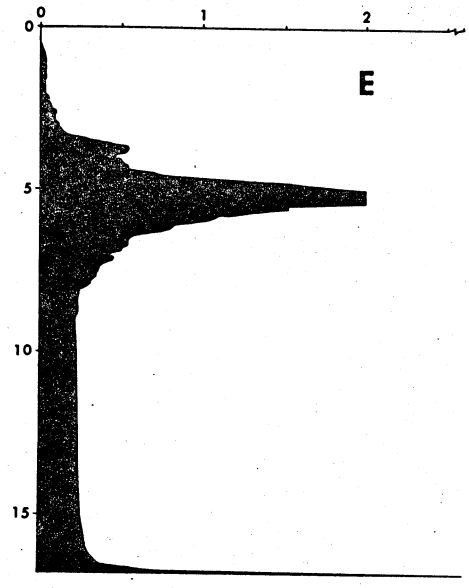
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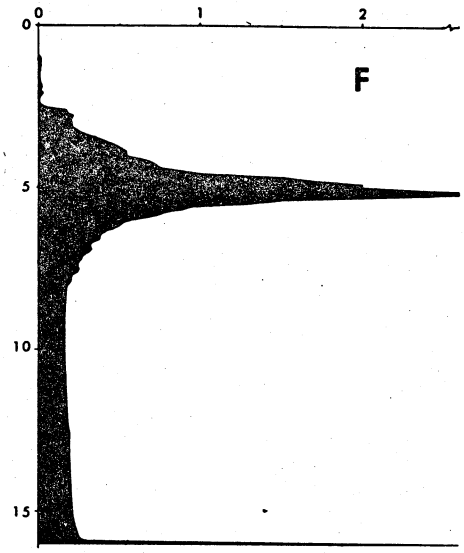
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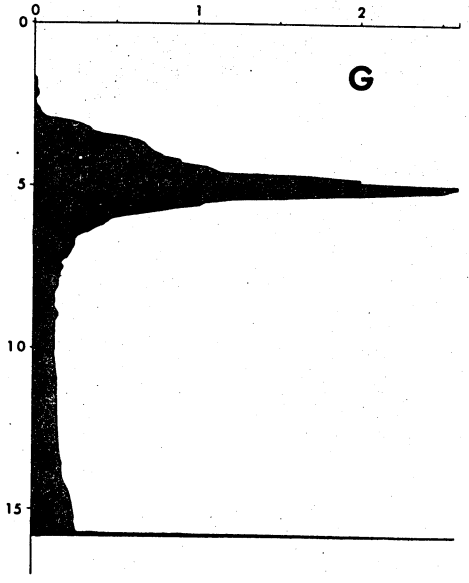
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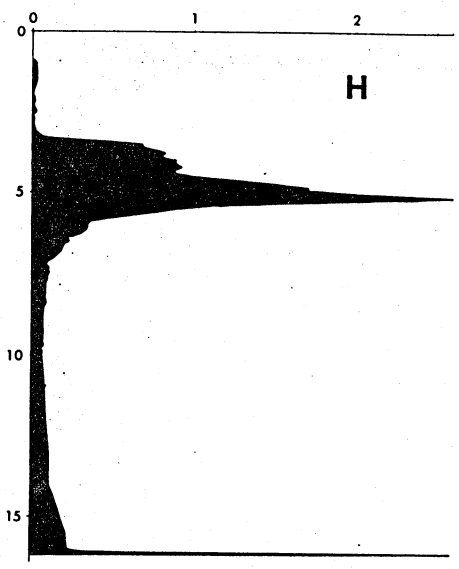
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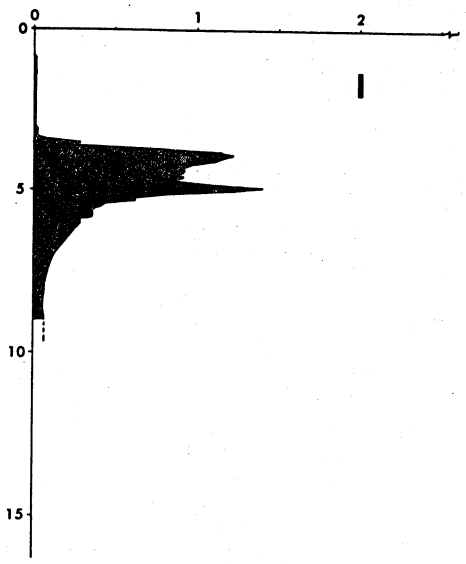
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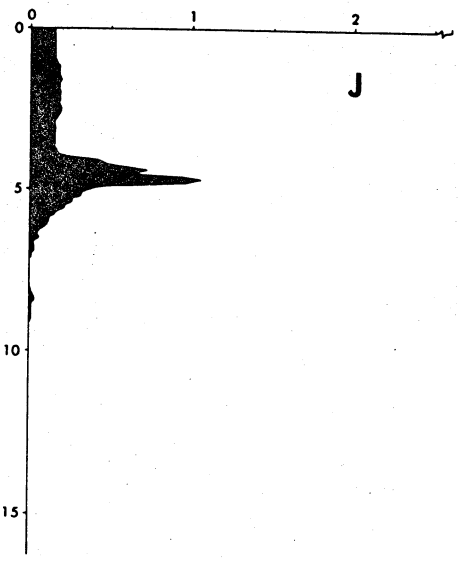
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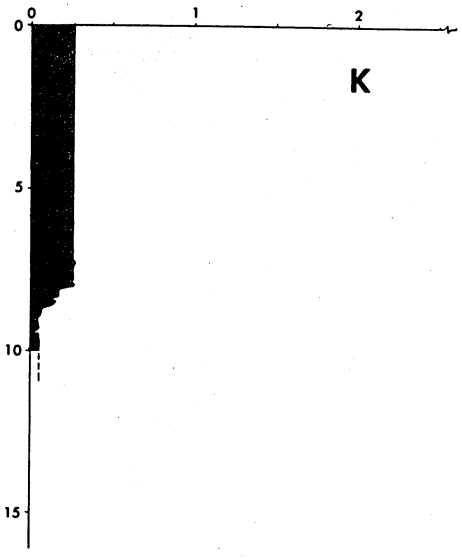
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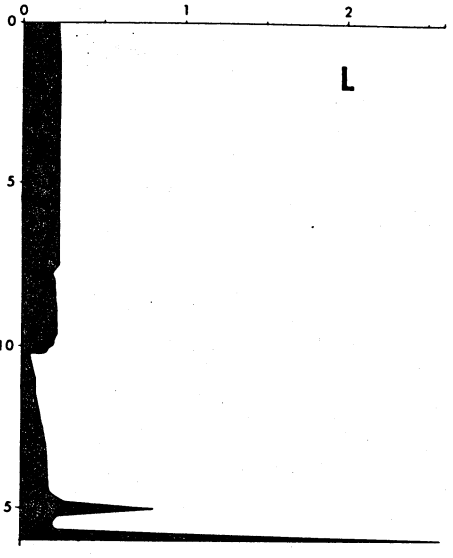
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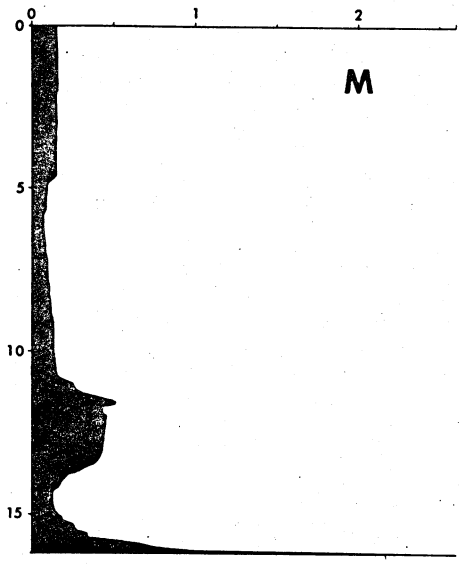
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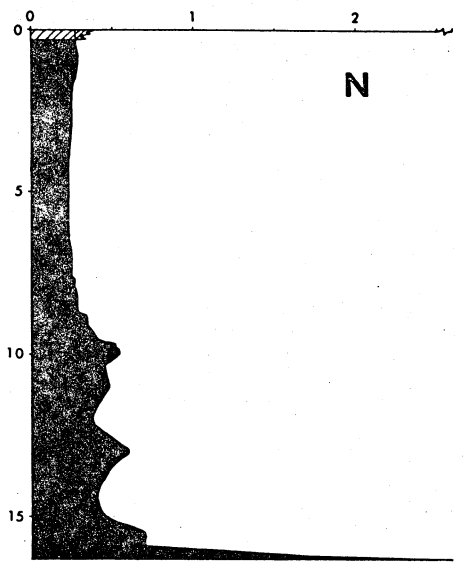
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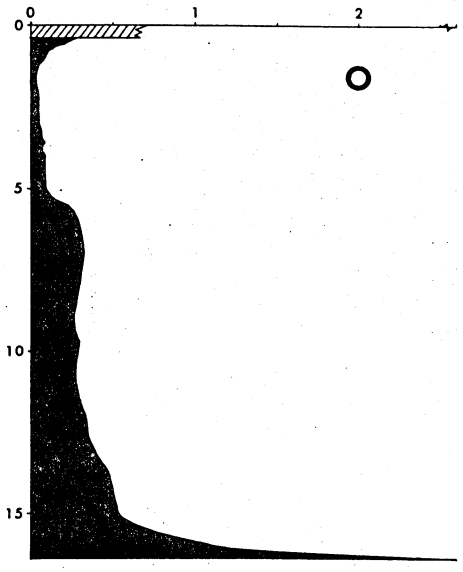
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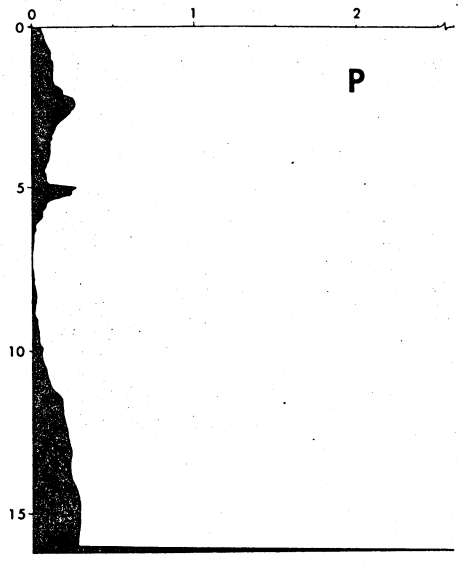
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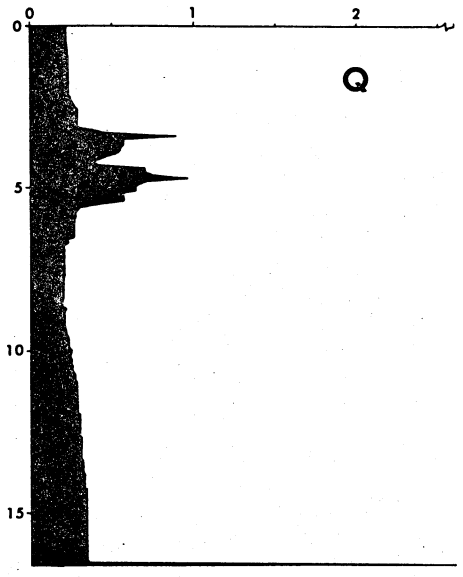
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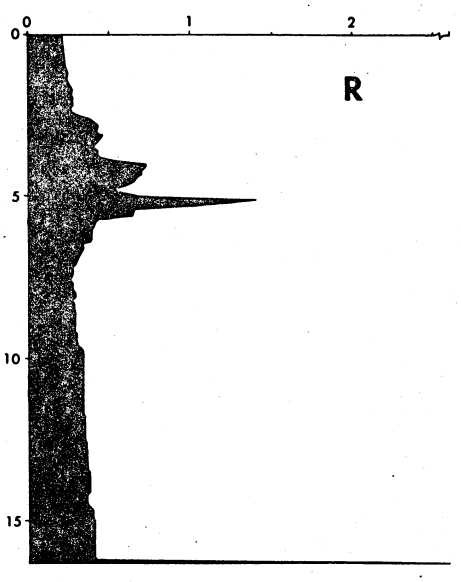
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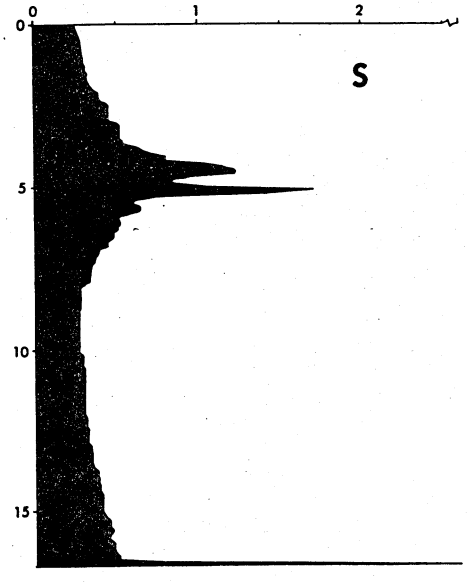
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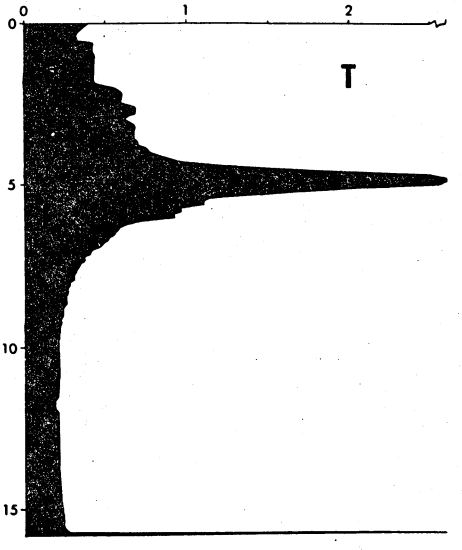
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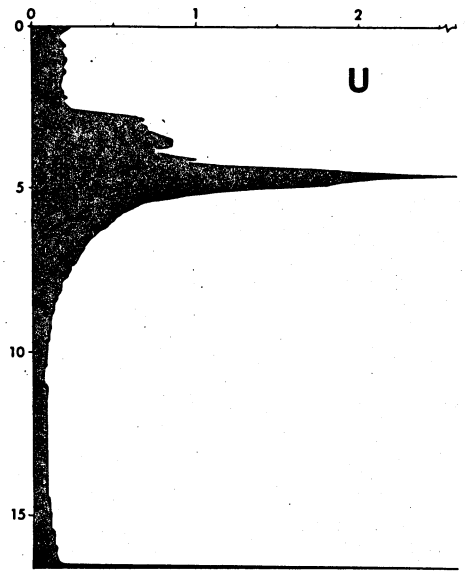
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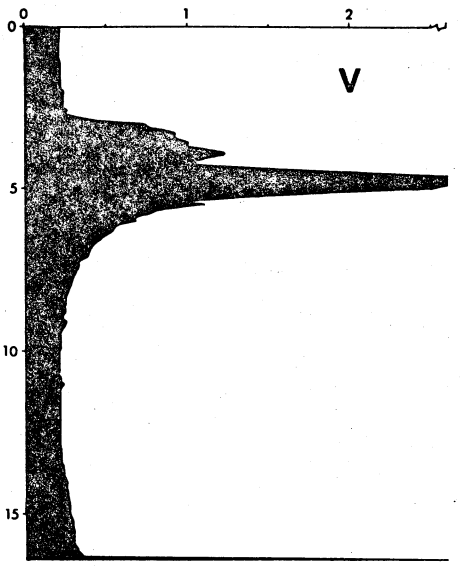
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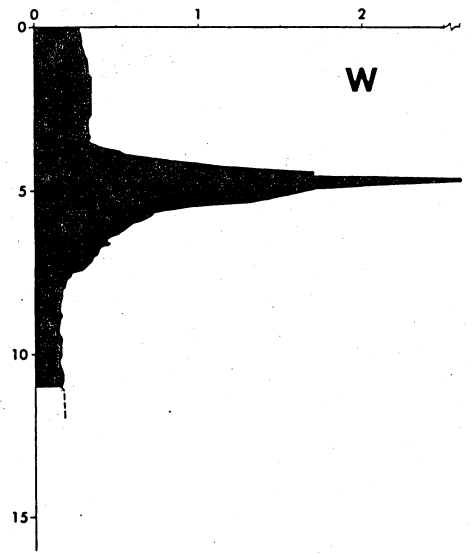
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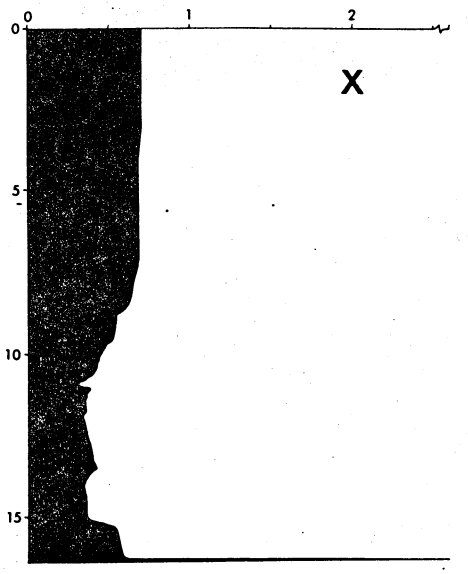
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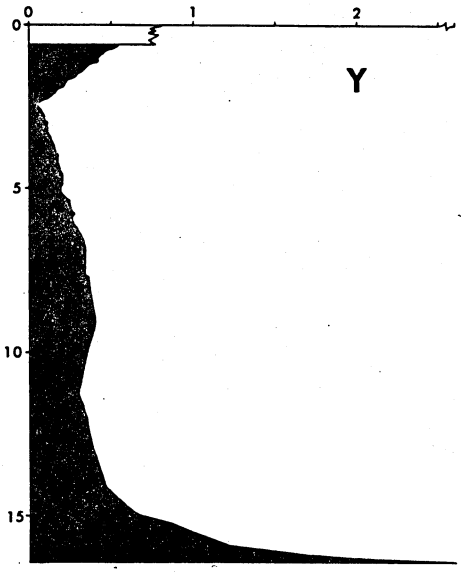
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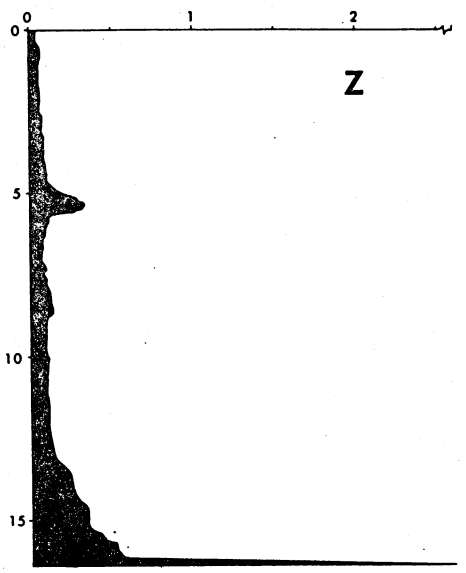
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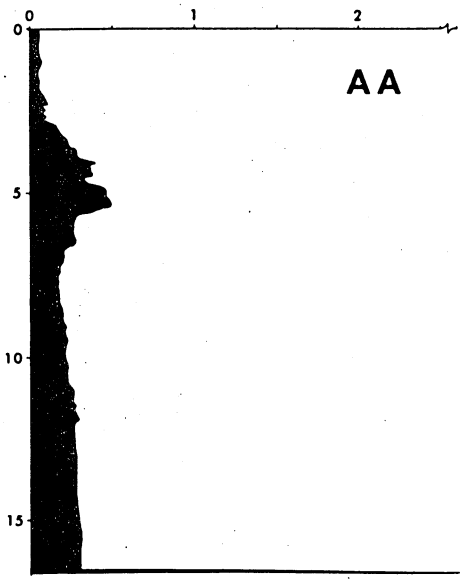
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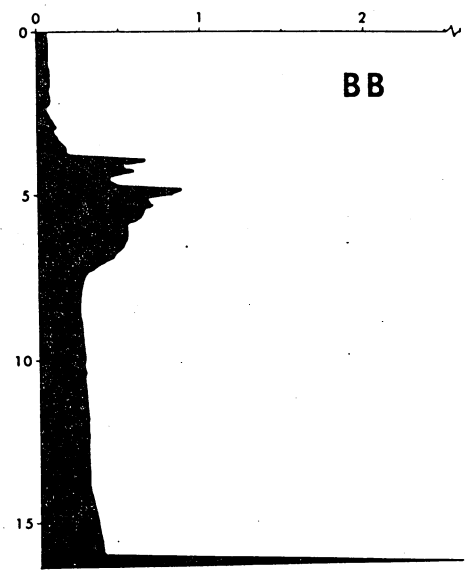
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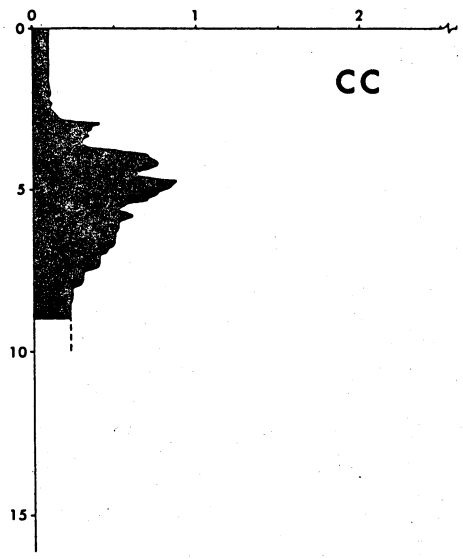
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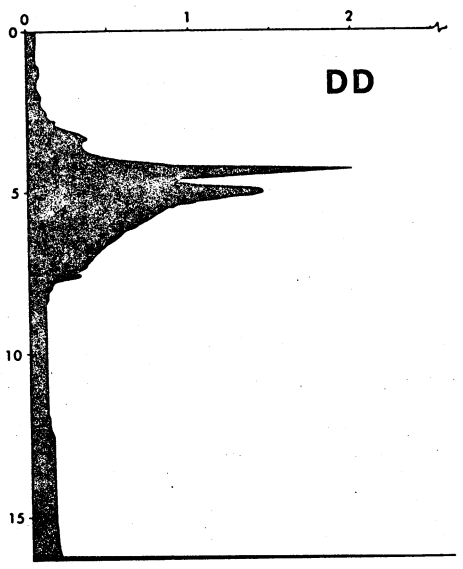
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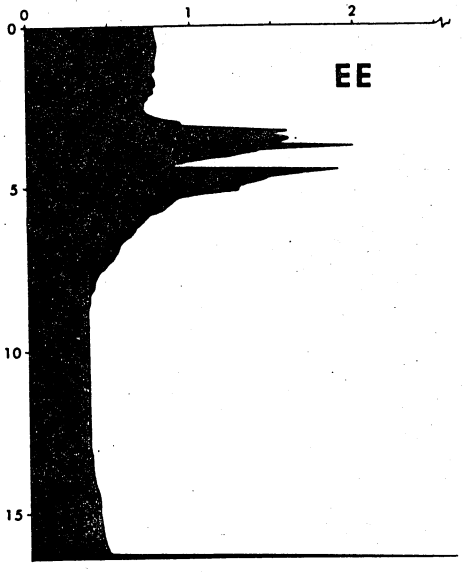
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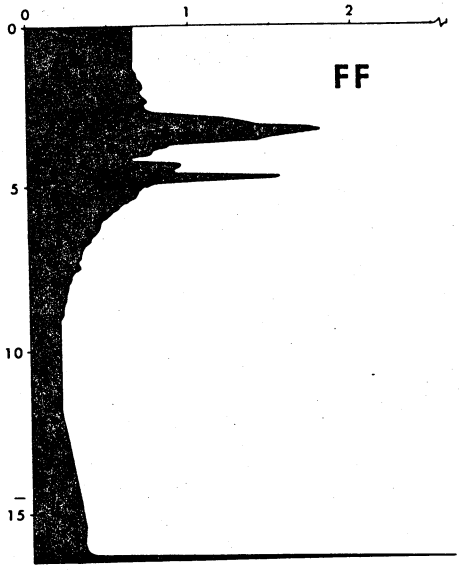
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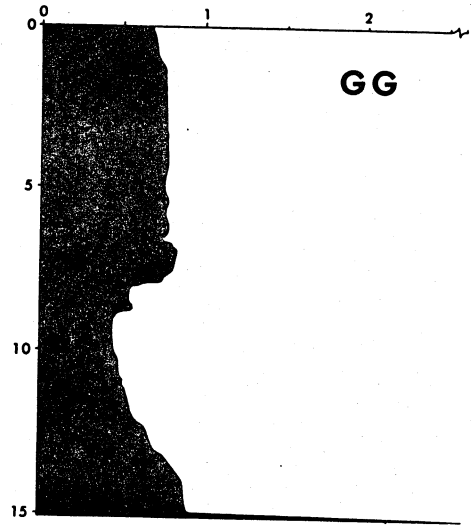
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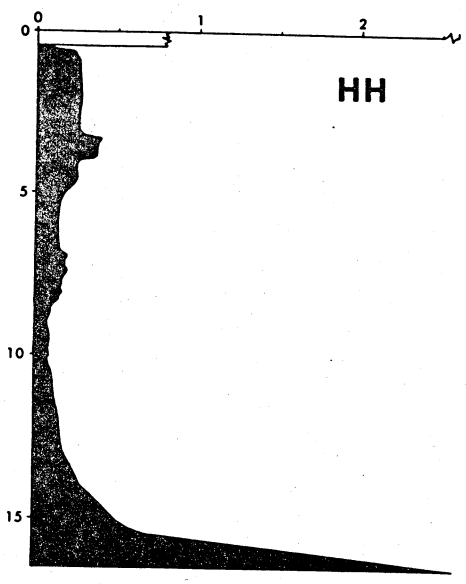
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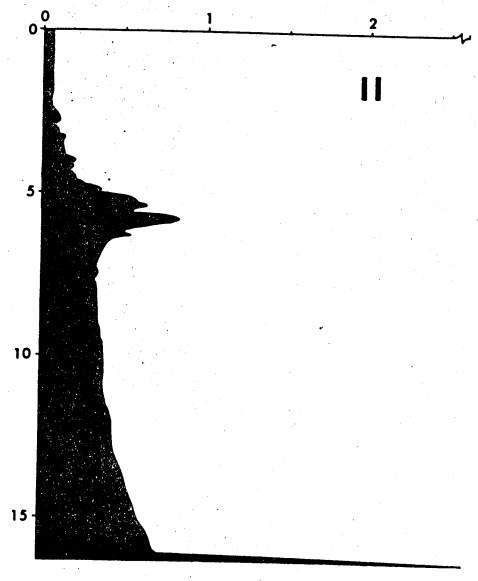
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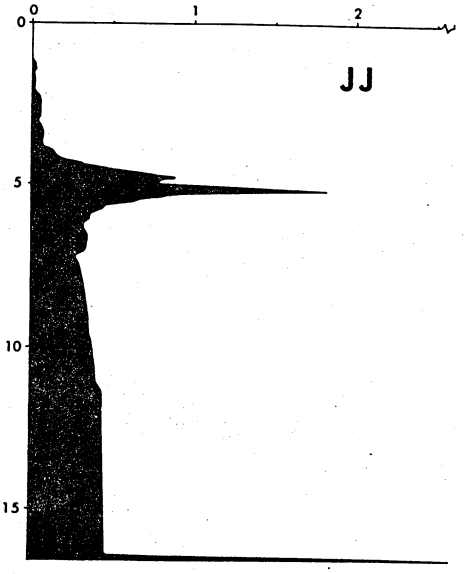
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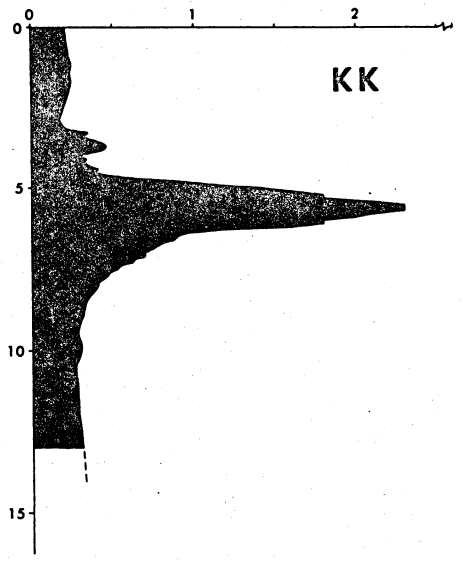
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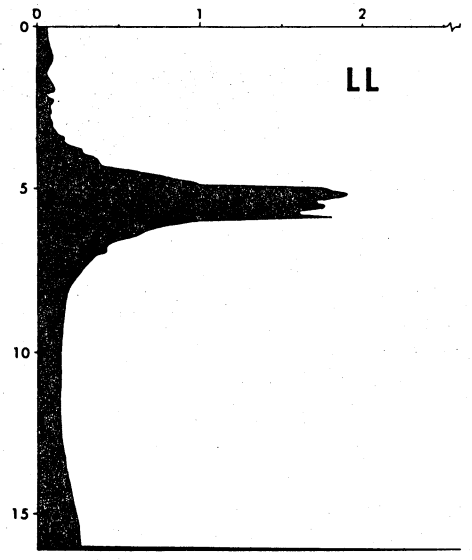
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LL
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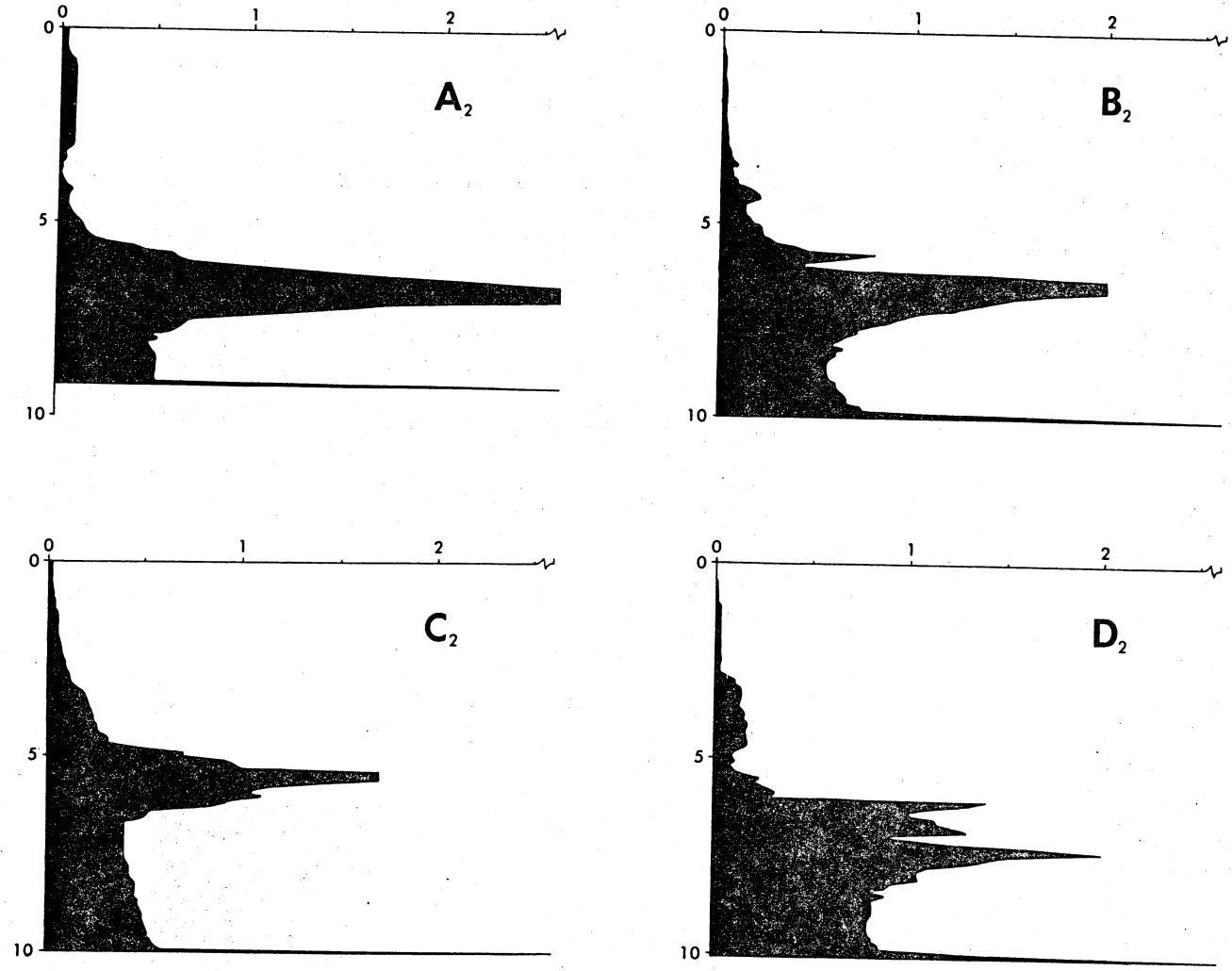
15

ARCO LAKE OPTICAL DENSITY PROFILES

A2	June 23, 1968
B2	August 5, 1968
C2	May 19, 1969
D2	June 5, 1969
E2	August 2, 1969
F2	August 16, 1969
G2	September 11, 1969
H2	May 3, 1970
I2	May 24, 1970
J2	June 13, 1970
K2	June 27, 1970
L2	July 9, 1970
M2	August 4, 1970
N2	August 15, 1970
O2	October 17, 1970
P2	April 10, 1971
Q2	May 10, 1971
R2	June 7, 1971
S2	July 20, 1971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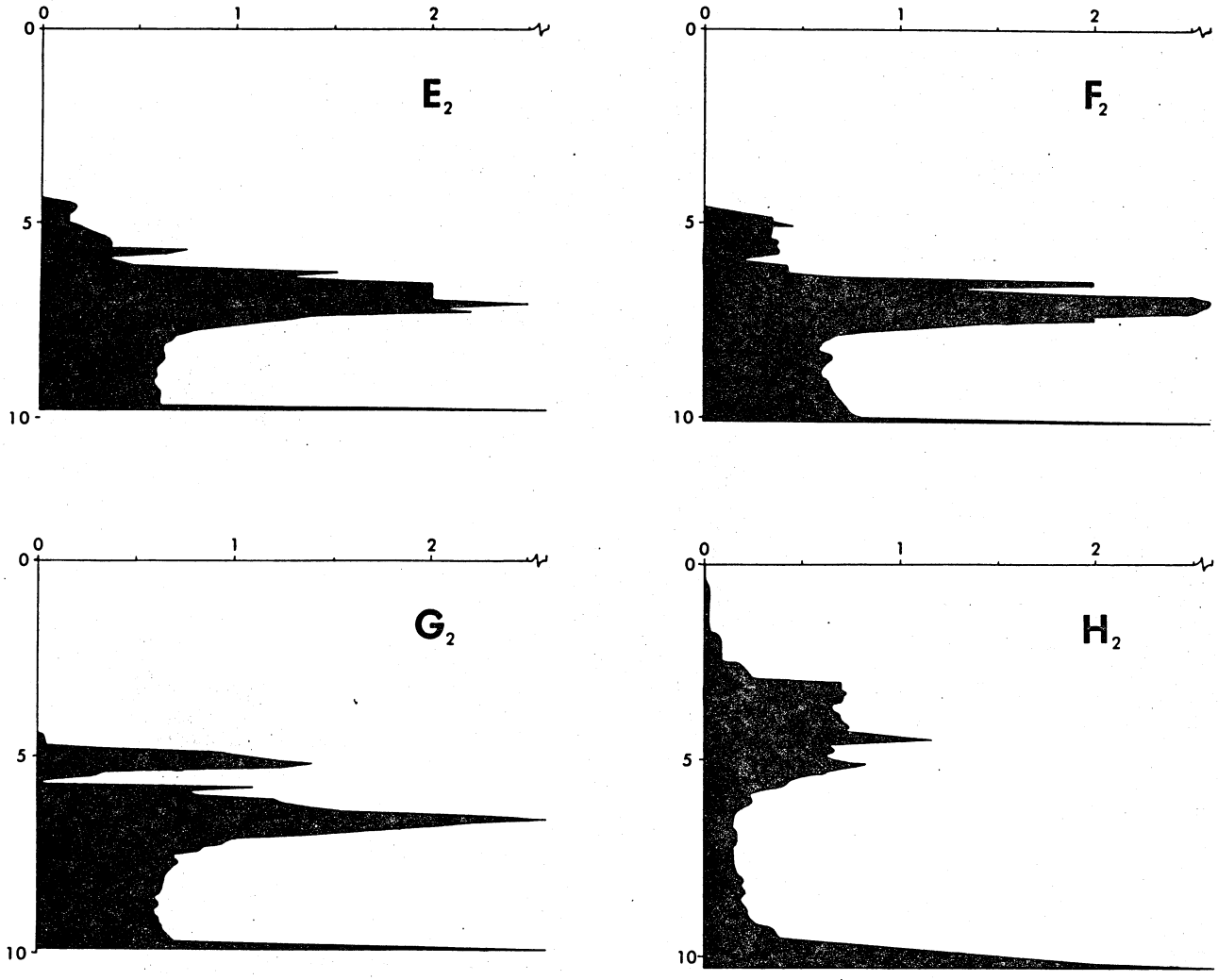
B2
C2
D2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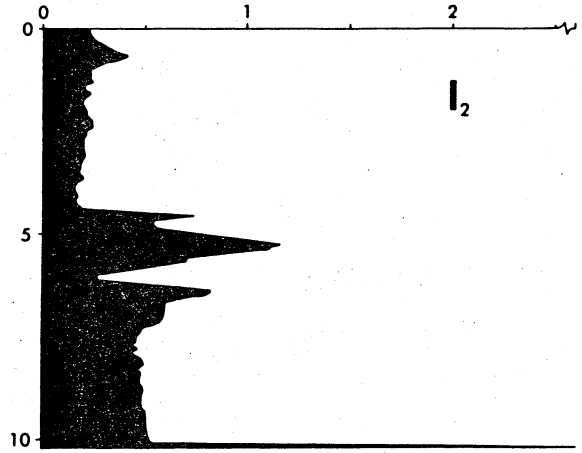
F_2
G_2
H_2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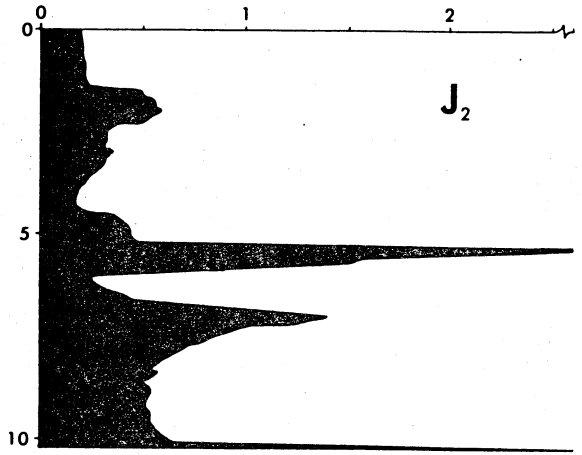
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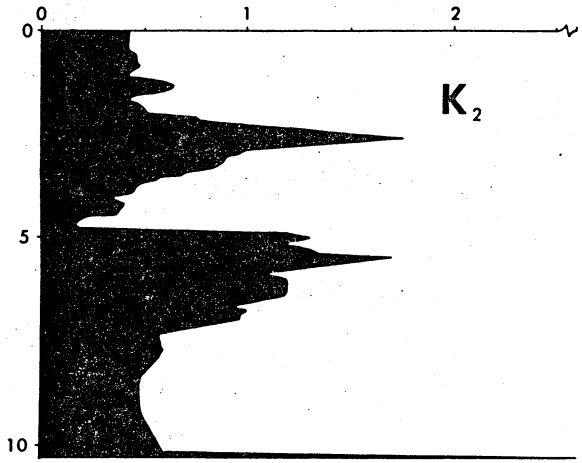
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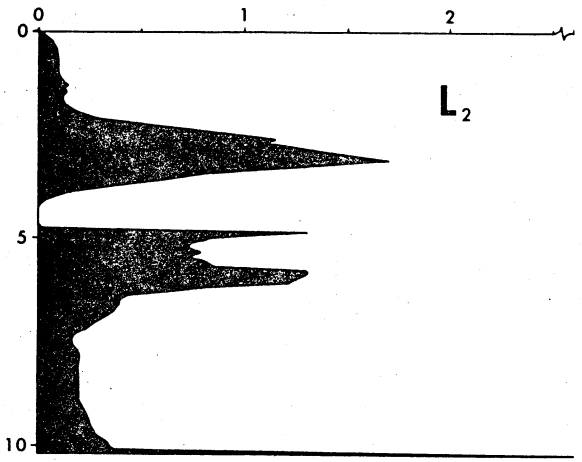
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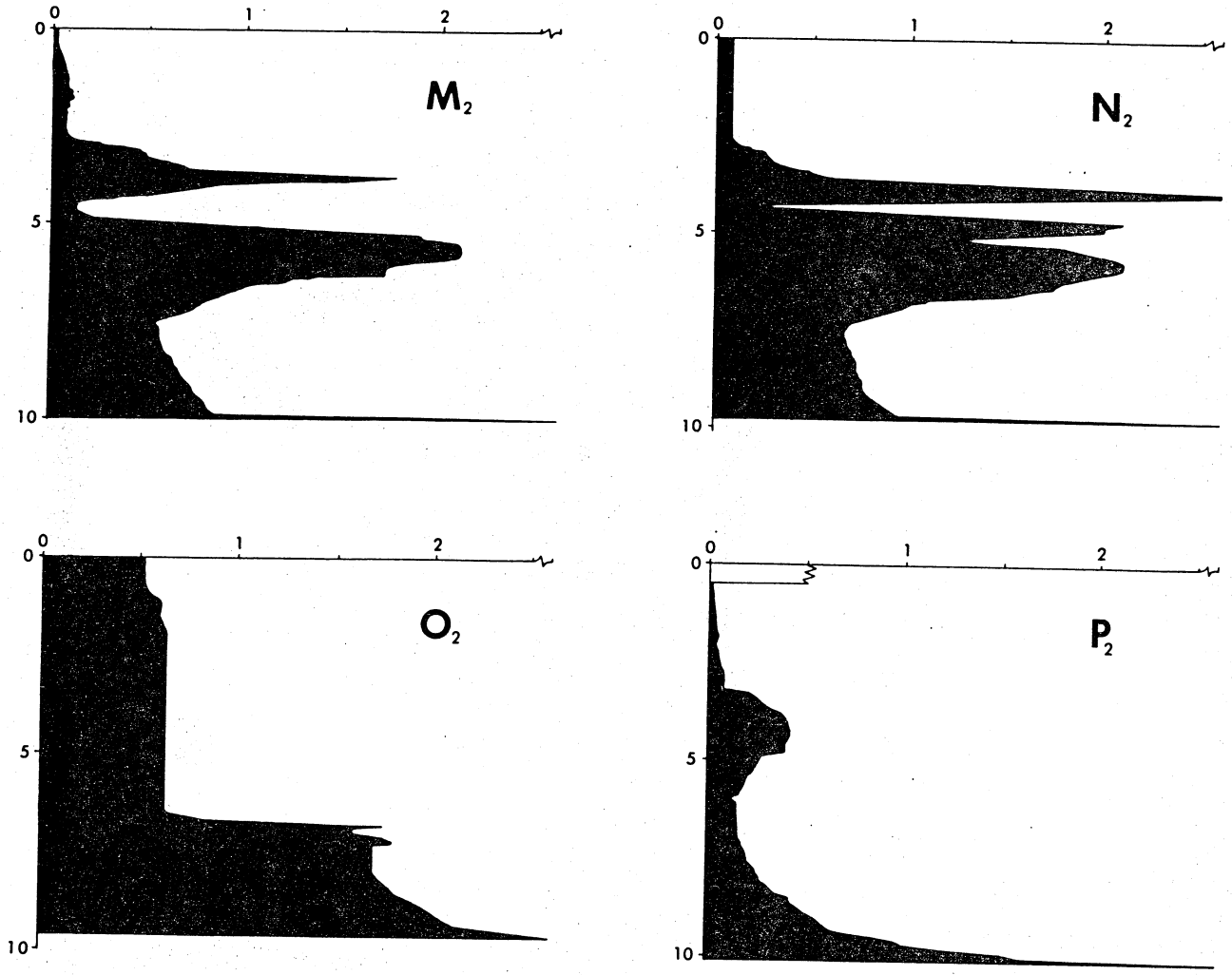
L_2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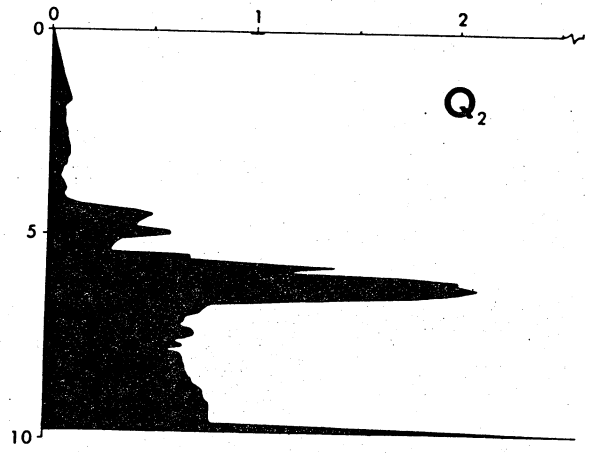
M_2
N_2
O_2
P_2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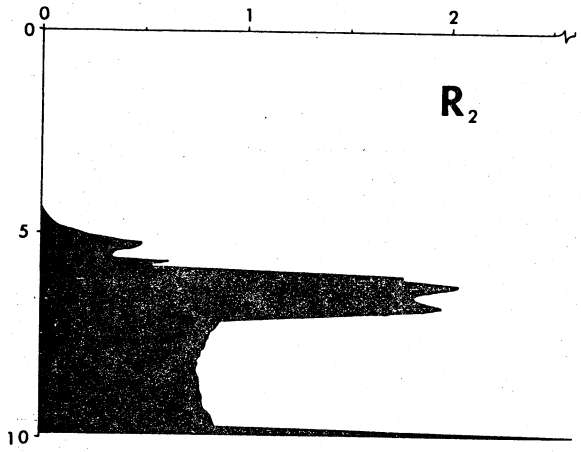
Q_2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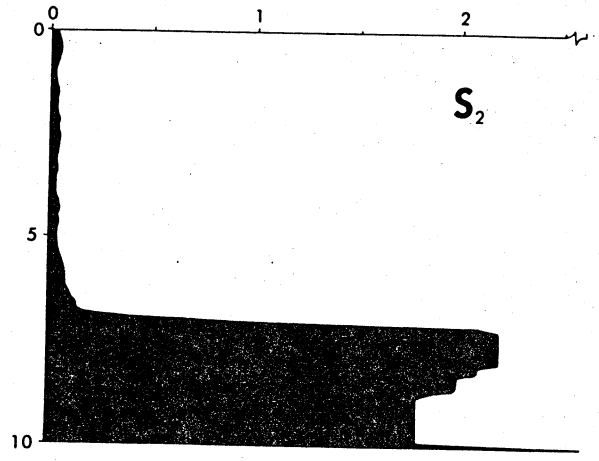
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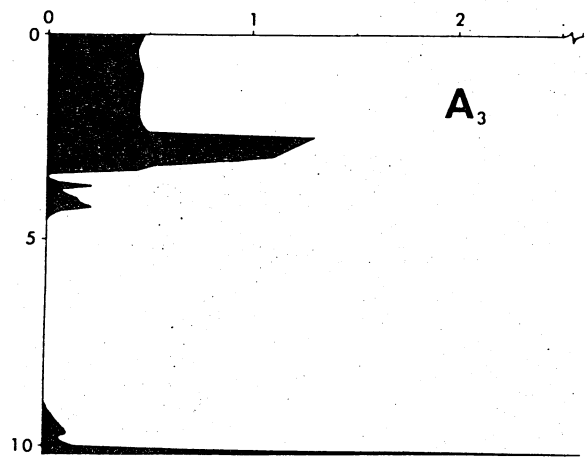
2
0
5
10
S_2

JOSEPHINE LAKE OPTICAL DENSITY PROFILES

A3	June 16, 1968	J3	July 9, 1970
B3	July 29, 1968	K3	July 21, 1970
C3	May 15, 1969	L3	August 4, 1970
D3	August 2, 1969	M3	August 15, 1970
E3	August 16, 1969	N3	October 17, 1970
F3	September 11, 1969	O3	April 9, 1971
G3	May 3, 1970	P3	May 10, 1971
H3	May 24, 1970	Q3	June 7, 1971
I3	June 27, 1970	R3	July 20, 1971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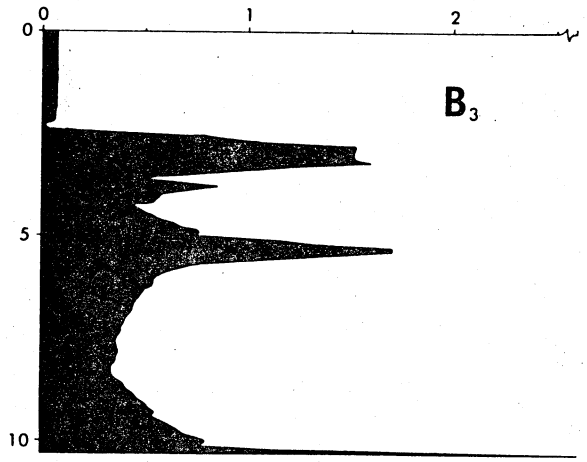
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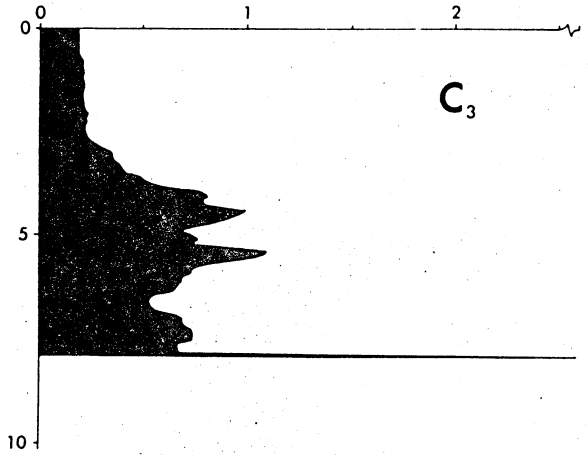
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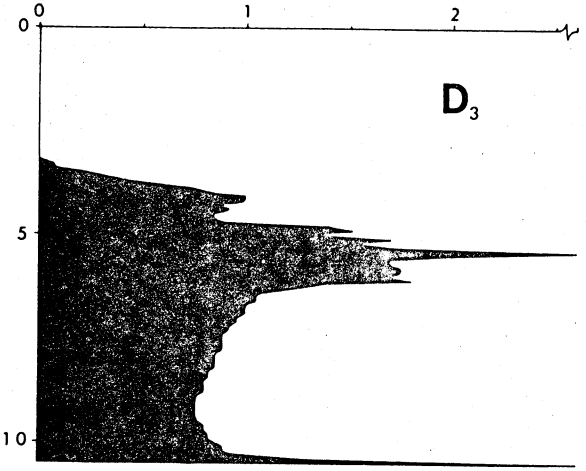
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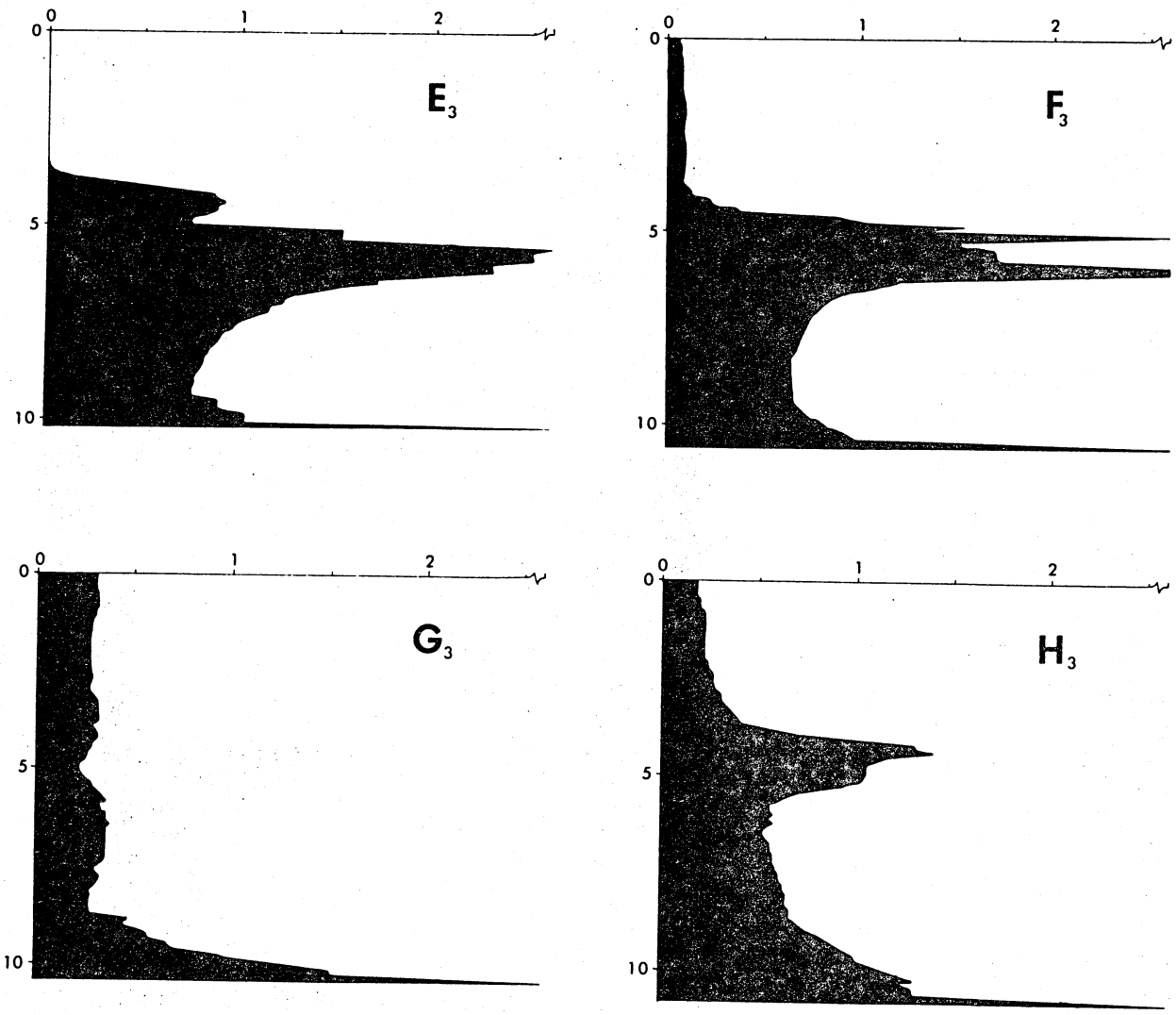
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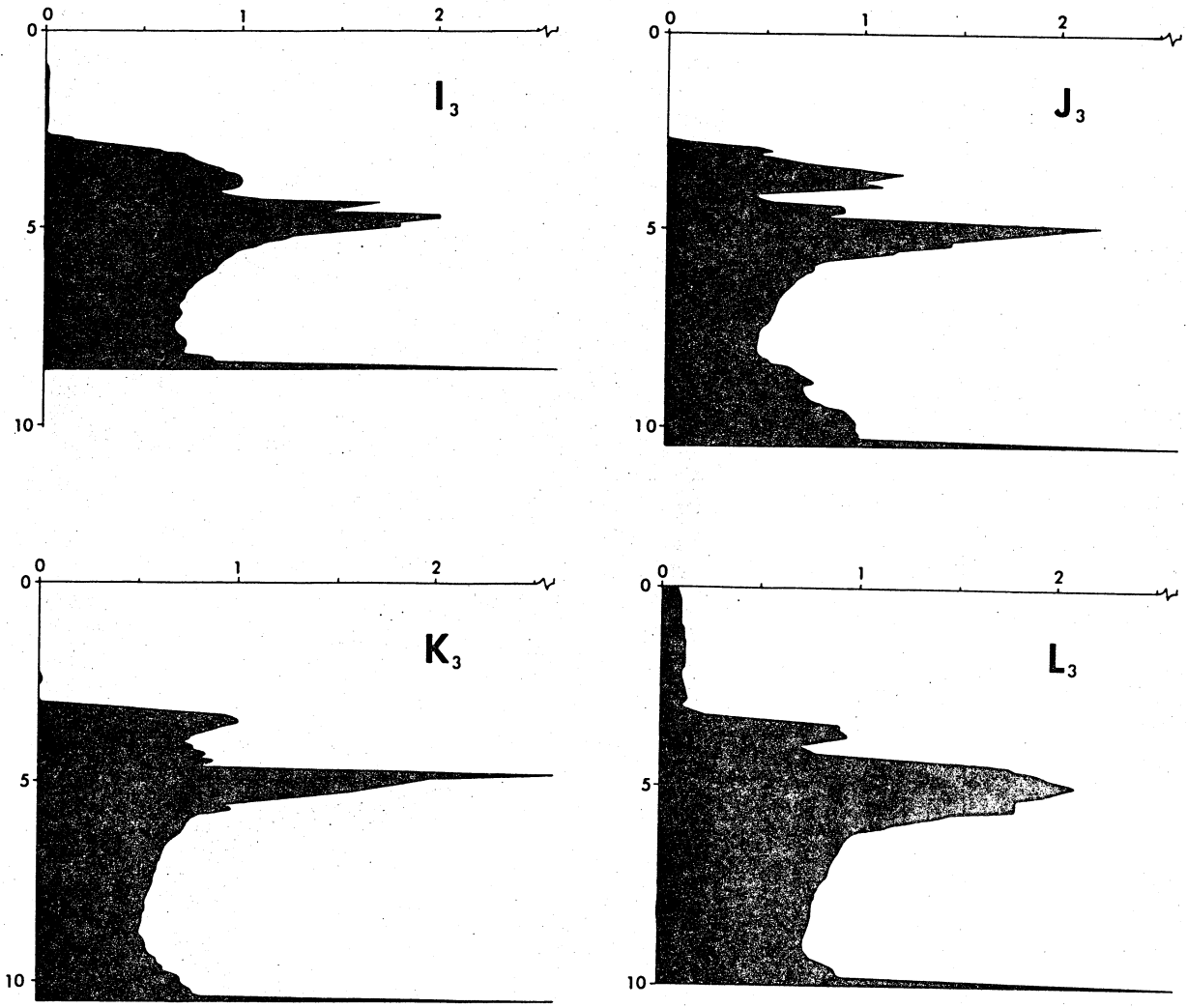
E_3
F_3
G_3
H_3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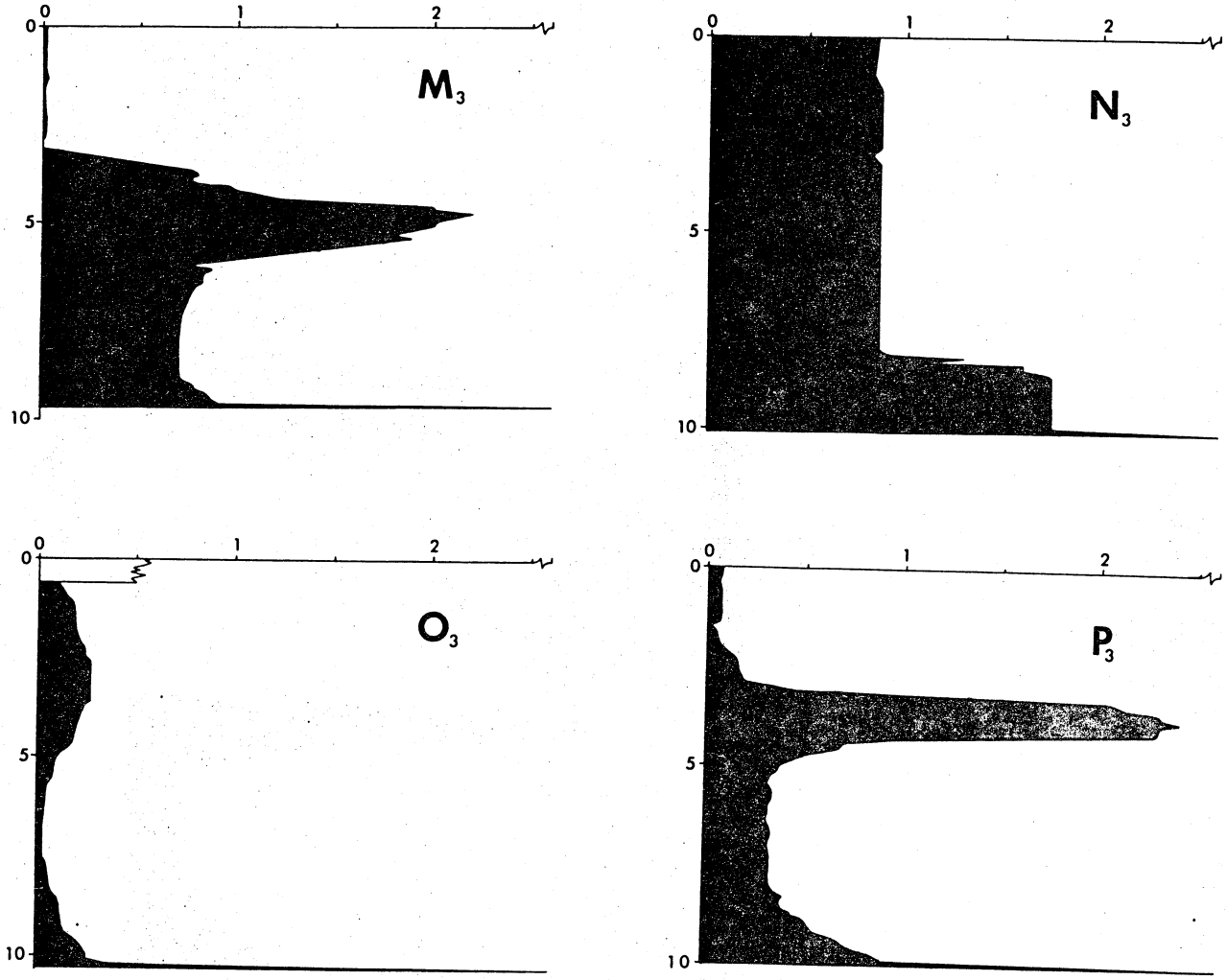
J_3
K_3
L_3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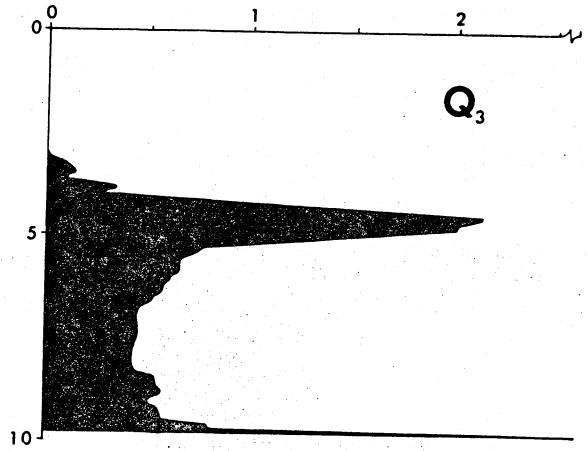
P_3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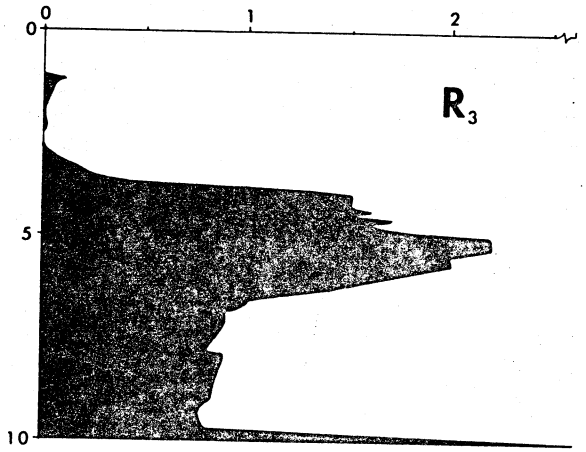
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R_3
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10

APPENDIX II. LIST OF SPECIES, CODE NUMBERS, AND UNIT VOLUMES USED IN TOTAL VOLUME DETERMINATIONS

The code numbers in the following list are those used in a computer program developed by the author, available upon request, for determining the various estimates of dominance mentioned in the body of the thesis, as well as community diversity. The volumes are in cubic micra.

CODE	SPECIES	VOLUME
CYANOPHYCEAE		
1	Merismopedia trolleri	57
2	Merismopedia tenuissima	40
3	Aphanocapsa delicatissima	300
4	Chroococcus limneticus	30
5	Rhabdoderma lineare	4
6	Synechocystis minuscula Woronichin	10
7	Gomphosphaeria naegelliana	11000
8	Gomphosphaeria lacustris	700
9	Coelosphaerium pallidum	500
11	Aphanothece clathrata	55
13	Gloeothece violacea	70
15	Microcystis incerta	30
16	Microcystis aeruginosa	3680
20	Oscillatoria agardhii Gom.	1100
21	Oscillatoria agardhii v. isothrix	5650
22	Oscillatoria redekei van Goor	630
23	Oscillatoria amphibia v. 1	300
24	Oscillatoria amphibia v. 2	400
25	Oscillatoria ornata	39290
26	Oscillatoria limnetica Lemm.	5000
27	Oscillatoria tenuis	1100

APPENDIX II continued.

CODE	SPECIES	VOLUME
28	Oscillatoria amphibia Ag.	600
29	Oscillatoria iwanoffiana Geitler	4860
30	Oscillatoria limmetica v. 1	255
31	Oscillatoria pseudo-geminata	110
32	Oscillatoria Iwanoffiana	10500
37	Phormidium tenue	102
41	Lyngbya limnetica	79
42	Lyngbya sp. subtiles W. West	157
43	Lyngbya sp. lacustris Lemm.	354
44	Lyngbya sp. cliarensis W. West	3182
45	Lyngbya lauterbornii	20
46	Lyngbya pseudospirulina	40
47	Lyngbya sp.	1386
51	Arthrospira abbreviata Lemm.	90
52	Arthrospira nordstedtii gom.	242
53	Arthrospira sp. 3	1232
56	Romeria leopoliensis (Racib.) Koczw.	340
61	Anabaena cylindrica	1260
62	Anabaena cylindrica v. 1	1260
63	Anabaena sp.	315
64	Anabaena sp.	2700
65	Anabaena sp.	630
66	Anabaena baltica J. Schm.	500
67	Anabaena wisconsinense	1332
68	Anabaena planctonica	8500
69	Anabaena affinis	3267

APPENDIX II continued.

CODE	SPECIES	VOLUME
70	Anabaena solitaria v. crassa	9600
71	Anabaena flos-aquae	2394
72	Anabaena spiroides v. crassa	9216
73	Anabaena spiroides Klebahn v. 1	622
74	Anabaena sp. 7	656
76	Anabaenopsis raciborskii	1156
77	Raphidiopsis sp.	1102
79	Aphanizomenon flos-aquae	1694
80	Aphanizomenon elenkinii	2410
CHLOROPHYCEAE		
101	Volvox globator	9000
103	Green microflagellates	98
105	Chlamydomonas altera	1131
106	Chlamydomonas sp. 1	1437
107	Chlamydomonas sp. 2	268
110	Scourfeldia cordiformis	200
115	Chlorogonium maximum	50000
128	Cerasterias staurastroides	350
129	Tetraedron caudatum	100
130	Coccoid green	7
131	Chlorococcus sp.	14
132	Tetraedron minimum	100
133	Tetraedron min. v. scrobiculare	279
134	Tetraedron muticum	681
135	Echinosphaerella sp. 1	100

APPENDIX II continued.

CODE	SPECIES	VOLUME
136	Lagerheimia cingula	100
137	Lagerheimia genevensis	100
138	Ankistrodesmus falcatus	60
139	Ankistrodesmus falcatus v. spirilliformis	15
140	Ankistrodesmus falcatus v. mirabilis	60
141	Franceia droescheri	100
142	Schroederia spp.	1120
143	Selenastrum sp.	100
144	Lagerheimia quadriseta	100
155	Dactylococcus infusorium	100
156	Dictyosphaerium elegans	57
157	Dictyosphaerium pulchellum	57
158	Dimorphococcus	100
160	Golenkinia radiata	200
161	Crucigenia tetrapedia	57
162	Crucigenia fenestrata	57
171	Scenedesmus quadricauda	656
172	Scenedesmus ecornis v. disciformis	656
173	Scenedesmus opoliensis	656
174	Scenedesmus bijuga	144
175	Scenedesmus dimorphus	276
176	Scenedesmus sp. 1	328
177	Scenedesmus obliquus	656
178	Scenedesmus bijuga v. alterans	656
179	Actinastrum hantzschii	320

APPENDIX II continued.

CODE	SPECIES	VOLUME
181	Pediastrum simplex	3500
182	Pediastrum boryanum	3048
183	Pediastrum duplex v. clathratum	4230
184	Pediastrum tetras v. tetraedron	1000
190	Quadrigula chodatii	5600
191	Oocystis sp.	500
192	Oocystis parva	620
193	Oocystis lacustris	248
195	Sphaerocystis schroeteri	496
196	Elakatothrix gelatinosa	136
197	Kirchneriella lunais	250
201	Coelastrum cambricum	1176
202	Coelastrum microporum	1176
203	Coelastrum reticulatum	1176
206	Trochisia aspera	632
215	Mougeotia sp.	1096
217	Ulothrix bacillarus	1500
221	Closterium sp.	880
222	Closterium aciculare	2624
223	Closterium sp.	1308
224	Closterium acutum v. variable	319
231	Staurastrum tetracerum	231
232	Staurastrum tetracerum v. subexcavatum	770
233	Staurastrum punctulatum	2078
234	Staurastrum muticum	329

APPENDIX II continued.

CODE	SPECIES	VOLUME
235	Staurastrum sp. 1	280
236	Staurastrum sp. 2	1500
237	Staurastrum sp. 3	6760
238	Staurastrum minimum	230
261	Cosmarium minimum	100
262	Cosmarium depressum	764
263	Cosmarium meneghini	1312
264	Cosmarium obtusatum	17750
265	Cosmarium granulosa	18000
281	Arthrodesmus sp. 1	536
282	Arthrodesmus sp. 2	600
283	Arthrodesmus sp. 3	1000
291	Desmidium sp. 1	550
CHRYSOPHYCEAE		
310	Dinobryon divergens	283
302	Dinobryon bavaricum	283
303	Dinobryon sociale	283
304	Dinobryon acuminatum	283
305	Dinobryon cylindricum	283
306	Dinobryon sertularia	283
307	Dinobryon divergens v. schauinslandii	283
309	Diceras sp. 1	283
310	Stylochrysallis sp. 1	283
311	Treubaria triappendiculata	283
312	Synura sp. 1	525

APPENDIX II continued.

CODE	SPECIES	VOLUME
314	Stenocalyx monolfera	50
321	Kephyrion cupuliforme	75
322	Kephyrion sp. 1	800
323	Kephyrion sp. 2	75
324	Kephyrion sp. 3	75
325	Kephyrion sp. 5	75
326	Pseudokephyrion cupuliforme	75
329	Chrysophycean flagellates	524
330	Chrysophycean microflagellates	30
331	Prymnesium sp.	525
341	Mallomonas sp. 1	500
	BACILLARIOPHYCEAE	
370	Stephanodiscus or Cyclotella	139
373	Stephanodiscus niagarae	17890
374	Cyclotella comta	4950
375	Cyclotella sociale	300
376	Attheya zachariase	3345
378	Rhizosolenia longiseta	1000
380	Melosira islandica	500
381	Melosira granulosa v. angustissima	1518
382	Melosira sp. 1	2825
390	Synedra ulna	5000
391	Synedra acus	1062
392	Synedra sp.	378
396	Fragilaria crotonensis	2076

APPENDIX II continued.

CODE	SPECIES	VOLUME
397	Fragilaria capitata v. mesolepta	1650
399	Tabellaria flocculosa	4000
400	Cocconeis placentula	3540
401	Asterionella formosa	3227
402	Fragilaria spp.	320
403	Diatoma	400
404	Fragilaria crotonensis	1500
405	Tabellaria fenestrata	500
421	Navicula sp.	1000
441	Nitzschia sp.	276
460	Stauroneis	200
462	Pleurosigma	57
CRYPTOPHYCEAE		
471	Cryptomonas erosa	600
473	Cryptomonas borealis	2000
475	Cryptomonad sp. 1	180
476	Cryptomonad sp. 2	128
477	Cryptomonad sp. 3	1890
478	Cryptomonad sp. 4	33
479	Cryptomonad sp. 5	5580
481	Bodo spora	25
486	Chilomonas sp.	100
487	Chilomonas sp. 2	600
491	Katablepharis ovalis	100

APPENDIX II continued.

CODE	SPECIES	VOLUME
DINOPHYCEAE		
501	Peridinium cinctum	20000
504	Glenodinium lacustre	992
506	Gymnodinium pulvisculus	472
511	Hemidinium sp.	500
514	Ceratium hirundinella	75210
EUGLENOPHYCEAE		
521	Euglena sp. 1	340
522	Euglena sp. 2	600
523	Euglena intermedia	800
531	Phacus sp. 1	500
541	Trachelomonas sp. 1	1412
UNIDENTIFIED		
561	Microflagellates (<2 micra)	6
562	Microflagellates (6 micra)	172
563	Unknown Cyst sp. 1	970
571	Mucilaginous bacterium	50

APPENDIX III. DAILY RECORD OF ATMOSPHERIC TEMPERATURE AT THE ITASCA (U.S.) WEATHER STATION (1960-1968)

The fold-out graph of daily temperature range is located in a pocket on the inside back cover. The data are taken from official records of the U. S. Weather Bureau.

As explained in the Introduction, the seasonal patterns in atmospheric temperature are reflected closely by summer epilimnetic temperatures in nearby lakes.

APPENDIX IV. A THREE-DECADE RECORD OF ICE-MELT ON LAKE ITASCA (1940-1970)

The following table is included as a permanent record mainly from a slip of paper left at the Itasca State Park Headquarters by former Park Superintendant Peterson.

The date of ice-melt from the study lakes was parallel but later than that from Lake Itasca. Ice-melt from Josephine Lake was always the most rapid of the study lakes (but at least a week after L. Itasca), then Deming, and finally Arco Lake. The order of ice-melt suggests that, at least in the size range of the Itasca Park lakes, the degree of exposure to wind is related to the rate of ice-melt. As the snow along the lake shores melted at least two weeks prior to the final ice-melt, the ground temperature rose rapidly. Wind would have carried re-radiated heat to the ice surface. Once open water developed along the shores of Lake Itasca, the remainder of the ice ablated rapidly during warm, windy days. Under similar conditions, the ice-melt in the smaller lakes was relatively slow.

The date of ice-melt is undoubtedly affected by a combination of air temperature, degree of snow cover, and wind activity. A comparison of the air temperature record (fold-out) with the date of ice-melt suggests that the factor of air temperature maximum, minimum, or median is not sufficient to predict accurately the date of ice-melt.

The maximum ice thickness in all Itasca Park lakes surveyed tended to be greatest on the larger lakes, where the snow cover was least (due to wind-sweeping). The overburden of snow after

large snowfalls frequently lead to seepage of lake water upward through cracks, forming slush conditions and "melt holes" (mistaken by many as caused by underwater springs). During years when heavy snowfalls occurred in November and early December (shortly after ice formation) the majority of ice was comprised of frozen slush (snow ice). Occasionally, lenses of water as much as 0.3 m deep persisted between layers of snow ice, until late winter melting.

Date of Ice-Melt from

Lake Itasca (1940-1969)

1940	April 29
1	" 14
2	" 18
3	" 23
4	May 1
1945	April 9*
6	" 11
7	May 1
8	April 22
9	" 20
1950	May 18**
1	" 1
2	April 23
3	" 25
4	" 23
1955	" 18
6	May 7
7	April 24
8	" 14
9	" 22
1960	" 24
1	" 28
2	" 28
3	" 15
4	" 25
1965	May 1
6	" 5
7	April 16
8	" 17
9	" 22
1970	No Data

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*Earliest recorded date.
**Latest recorded date.

NOTE: By 4-day classes, the highest frequency of ice-melt during 1940-69 was April 21-24. The 1940-66 record was supplied by Andrew Peterson, former park superintendant.

ITASCA BIOLOGICAL STATION
TEMPERATURE RECORD
DAILY MAX - MIN
GRAPH: [illegible]

Daily Temperature Range

Lake Itasca, Minn. Weather Station

ICE OUT

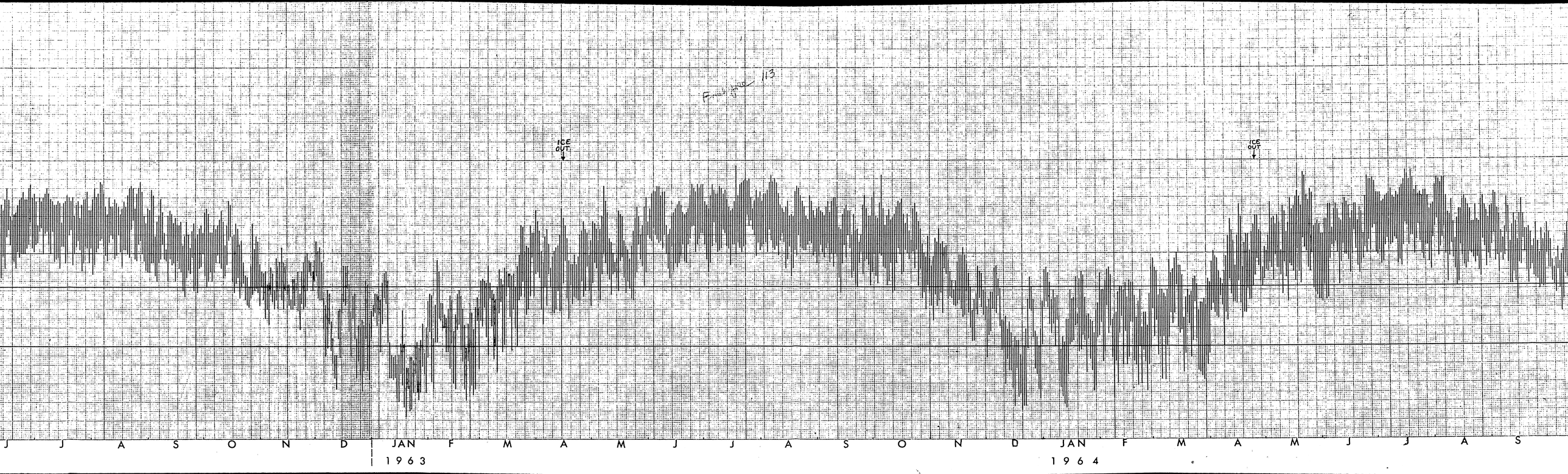
ICE OUT

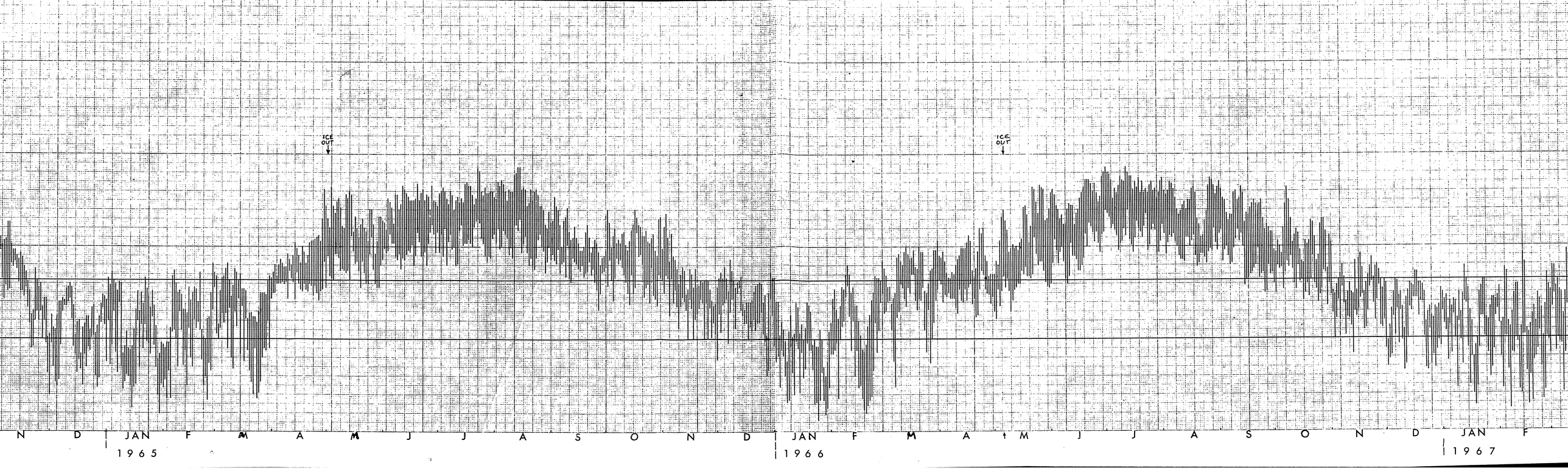
°C °F

1960

JAN F M A M J J A S O N D JAN F M A M J J A S O N D JAN F

1960 1961 1962


ICE OUT
ICE OUT
J J A S O N D JAN F M A M J J A S O N D JAN F M A M J J A S
1963
1964


ICE OUT
ICE OUT
N D JAN F M A M J J A S O N D JAN F M A M J J A S O N D JAN F
1965
1966
1967